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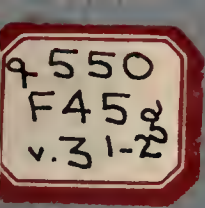
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THE VERTEBRATE FAUNA OF THE SELMA FORMATION OF ALABAMA

PART I. INTRODUCTION

PART II. THE PLEURODIRAN TURTLES

RAINER ZANGERL

FIELDIANA: GEOLOGY MEMOIRS

VOLUME 3, NUMBERS 1 AND 2

Published by

CHICAGO NATURAL HISTORY MUSEUM

APRIL 30, 1948

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SELMA FORMATION OF ALABAMA

PART II. THE PLEURODIRAN TURTLES

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RAINER ZANGERL

CURATOR OF FOSSIL REPTILES

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CONTENTS

	PAGE
LIST OF ILLUSTRATIONS	21
INTRODUCTION	23
DESCRIPTION OF <i>PODOCNEMIS ALABAMAE</i> , SP. NOV.	25
Description of Materials	26
Plastron	33
Shoulder Girdle and Humerus	34
Pelvis	34
Measurements	35
Systematic Relationships	39
SUMMARY	52
REFERENCES	55

LIST OF ILLUSTRATIONS

PLATES

4. Carapace, plastron, and sacral part of shell of *Podocnemis alabamae*.

TEXT FIGURES

	PAGE
3. Carapace and plastron of <i>Podocnemis alabamae</i>	27
4. Peripheral plates of <i>Podocnemis alabamae</i>	29
5. Nuchal and pygal plates, with adjoining peripherals, of <i>Podocnemis alabamae</i>	32
6. Ventral aspect of middle portion of carapace of <i>Podocnemis alabamae</i> .	35
7. Ventral aspect of anterior portion of carapace of <i>Podocnemis alabamae</i> .	43
8. Longitudinal and cross sections through first neural bone of <i>Podocnemis alabamae</i>	44
9. Ventral view of posterior portion of carapace of <i>Podocnemis alabamae</i> .	45
10. Outer view of left hyo- and mesoplastron of <i>Podocnemis alabamae</i> . .	46
11. Visceral view of xiphiplastral end of plastron of <i>Podocnemis alabamae</i> .	47
12. Lateral view of right ischium and pubis of <i>Podocnemis alabamae</i> . . .	49
13. Right humerus of <i>Podocnemis alabamae</i>	49
14. Morphological type patterns of pelomedusid, pelusiine, and pelomedusine turtle shells	50
15. Morphological affinities among pelomedusine turtles	51
16. Morphological affinities among pelomedusid turtles	53

The Pleurodiran Turtles

INTRODUCTION

Among the turtle remains collected in the lower Selma marls there are a few specimens readily distinguishable from all the rest by the thickness of the plates. All but one of these specimens were found exposed on the surface, broken into many more or less bleached fragments (pl. 4, fig. 1). It was recognized in the field that these bones belonged to a pleurodire turtle, with the xiphiplastron showing pronounced ischio-pubic scars and the hyo- and hypoplastra separated in the region of the bridge by mesoplastral plates.

The fragments of three of the specimens proved well enough preserved to permit the reassembling of fairly complete shells. The other individuals are either badly weathered or consist of only small portions of the skeletons. Isolated bones of the shell of this species are rare in comparison with the occurrence of fragmentary remains of other forms. Associated with some of the specimens were parts of the shoulder girdle, the humerus, the pelvis, and several unidentifiable pieces of limb bones. Unfortunately, not a single skull was found with any of these remains and it can be stated with little probability of error that none of the isolated finds of turtle skulls, lower jaws, humeri, and scapulae in the collection belong to this species.

Altogether, parts of seven specimens were collected. All of them were found in the region of Harrell Station, but this is probably due to the limited extent of the outcrops elsewhere rather than to accidental preservation of an aggregation, or to restriction of the species to a particular stratigraphic horizon within the lower Selma beds, although these possibilities cannot be excluded.

As soon as the preparation of the better specimens approached completion it became evident that these forms are very similar to the materials collected by Mr. Barber in the Brownstown marl of Arkansas and subsequently described by Schmidt (1940) as *Podocnemis barberi*. In spite of the great degree of similarity, there are a number of constant differences by which the Alabama form can readily be distinguished from *P. barberi*, thus requiring the erection of a new species. Certain differences between the Alabama specimens, although rather considerable, can be explained as due to individual variation and age differences.

Order TESTUDINATA

Suborder PLEURODIRA

Family PELOMEDUSIDAE

Podocnemis alabamae sp. nov.

Type.—C.N.H.M. No. P27370, a nearly complete shell with pelvis. Collected by C. M. Barber, May, 1946.

Referred specimens.—C.N.H.M. No. P27369, a nearly complete carapace, most of the plastron and other skeletal fragments. Specimen is somewhat larger than type. Collected by C. M. Barber, May, 1946.

C.N.H.M. No. P27372, a smaller specimen consisting of most of the carapace and part of the plastron. Collected by R. Zangerl and W. D. Turnbull, May, 1946.

C.N.H.M. No. P27331, posterior portion of the carapace of a very small individual. Collected by Mrs. A. Zangerl, November, 1945.

C.N.H.M. No. P27406, largest, but very fragmentary specimen, badly weathered. Collected by C. M. Barber, May, 1946.

C.N.H.M. No. P27405, fragmentary, badly weathered specimen, about the size of P27369. Includes a humerus and parts of both carapace and plastron. Collected by Mrs. A. Zangerl, November, 1945.

C.N.H.M. No. P27419, two peripherals of a very small individual, about the size of P27331. Collected by C. M. Barber, October, 1946.

Horizon and Locality.—Lower, marly member of the Selma formation, late Cretaceous. All specimens were collected in exposures of the Harrell Station area (see pl. 3), southeast of Marion Junction, Dallas County, Alabama.

Diagnosis.—Proportions of shell as a whole and of constituent parts closely resembling *Podocnemis barberi*; number of neurals varying from six to seven. Scars of spinous processes of ninth and tenth vertebrae separated by shallow, saddle-shaped ridge, not united as in *P. barberi*; low, rounded, transverse ridges between free proximal ends and buttress scars of first and second costal ribs more pronounced than in *P. barberi*; anterior edges of epiplastra blunt, sometimes with broadly rounded swelling on either side of the sagittal suture; scales probably wider in comparison to length than in *P. barberi*.

Description of Materials

In publishing literature dealing with fossil turtles many authors neglect to furnish a clear description of the extent of the preserved bones. Such information is highly desirable, since it is often impossible to tell from the illustrations which parts of the skeleton are preserved in situ and which have been reconstructed. The following account gives an adequate description of the preserved parts of all individuals of the series.

The type specimen is a fairly large shell, on the whole well preserved, but some of the plates have been crushed, others distorted. During preparation no attempt was made to compensate for obvious or assumed distortions; thus, the outline of the shell (pl. 4, fig. 1) is probably different from what it was in life. The carapace, well arched both transversally and longitudinally, is distinctly higher than in the type specimen of *P. barberi* and all other individuals of the Alabama species. As a rule, turtle shells tend to flatten out during fossilization, rather than to become more highly arched. Thus it appears likely that the curvature of the carapace of the type specimen resembles most closely the original state.

The shell lacks right peripherals 3, 4, 10, and most of 11. On the left side the eighth marginal is missing and some of the remaining peripherals are crushed or damaged. The sixth neural is absent. The three posterior, left costal plates are more or less incomplete. The posterior margin of the suprapygal is broken off, so that the over-all length of the shell cannot be determined with certainty. The space between the broken posterior end of the suprapygal and the anterior margin of the pygal (now filled with plaster) is probably somewhat too wide. It was determined by the sutural contacts of left peripherals 9-11 and the pygal. Peripheral 9 made good sutural contact with the distal ends of the sixth and seventh costal plates. Some amount of distortion probably accounts for the fact that the pygal now lies in a slightly asymmetrical position. The plastron is essentially complete except for the posterior tips of the xiphiplastra. The constituent bones evidently became disarticulated before burial. The sutures are completely filled with matrix that could not be entirely removed and consequently had to be left widely open when the plastron was assembled. Besides the shell, the type specimen furnishes the dorsal portion of the right ilium, the right ischium, and both pubes. The anterior free processes of the pubes and the medial process of the ischium that meets its mate in the midline are broken off (fig. 12). The acetabular surfaces have suffered so badly that they can scarcely be recognized.

The carapace of P27369 is fairly complete; peripherals 5 and 8 as well as minor parts of 1, 3, 4, 6, 7 and 10 of the right side are missing. On the left side the fourth and parts of the third, fifth, sixth, seventh, eighth, and tenth marginal plates are lacking. Furthermore, the pygal is not quite complete; the fifth and seventh neurals, and parts of the right third, fourth, fifth, and sixth and the left second, third, and sixth costal plates were not recovered. The peripherals of the bridge region are crushed dorso-ventrally. In the plastron the bones remained intact during burial. A large portion of it is lacking, but fortunately none of the more important regions. Associated with this specimen are parts of both scapulae. The left one is the more complete. It lacks parts of both the dorsal and medial processes and the glenoidal surface is weathered.

The best-preserved bones belong to the carapace of P27372. It lacks the right costals 3, 5, and 6, all but the first and fourth neurals, the nuchal and pygal plates and peripherals 1 to 3 and 10 and 11 on the right side and 1 and 2 on the left. The peripherals do not show any visible signs of distortion. The plastron consists of both hyoplastra with the left mesoplastron attached, and the entoplastron.

P27406, the largest individual of the series, consists of fragments of all regions of the shell, but most pieces are weathered and of little value. Among the fragments are pieces of the shoulder girdle and of limb bones, including a left scapula with both processes broken

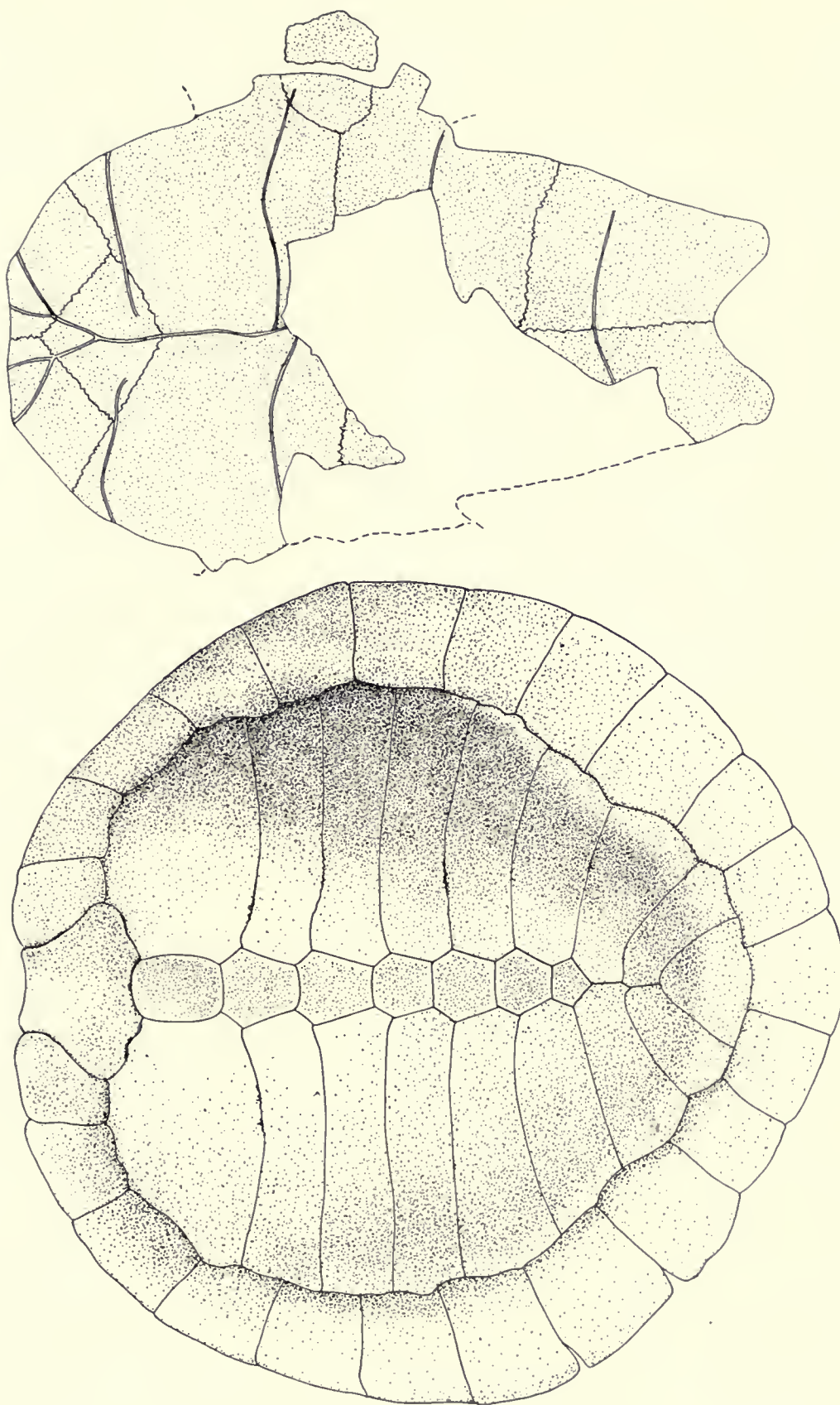


FIG. 3. Carapace and plastron of *Podocnemis alabamae*, C.N.H.M. P27369. None of shield furrows are preserved on carapace.

away and the proximal end of the right humerus. About half of the caput humeri is preserved, but the radial and ulnar processes are broken off. Another piece was tentatively identified as the proximal end of the right tibia.

P27405, although very fragmentary, is of interest because the seventh neural and parts of the sixth and adjoining costals are preserved, besides sizable portions of the plastron. Associated with this specimen is an exceptionally good humerus.

P27331 consists of costal plates 5 to 8 on both sides, and P27419 of the left eighth and ninth peripherals and some unidentifiable fragments.

The anterior margin of the carapace is notched, as in *P. barberi*. In the type specimen the notch is almost as distinctly expressed as in that species, but in P27369 it is very shallow. The nuchal plate of P27369 is hexagonal and its proportions are nearly identical with those of *P. barberi*. In the type specimen, however, the nuchal is relatively much wider and shorter (fig. 3; pl. 4, fig. 1). The medial aspect of the nuchal of P27370 along with a sagittal section are shown in figure 5. The number of neural plates can definitely be determined as varying between six and seven. P27369 and P27405 have seven neurals; the type, P27372, and P27331 have definitely six only. The first neural is four-sided, with the sides rounded. It is slightly longer than wide. The remaining neurals are hexagonal except the last, which is pentagonal. In P27369 the seventh neural is missing, but all the adjoining bones were recovered, so that its former presence is certain. In P27405 the seventh neural is preserved, together with portions of the adjoining bones. Its shape is exactly as indicated by the surrounding plates in P27369. The visceral surfaces of the neural bones are very well preserved in the type specimen and in P27372. Slightly distorted neurapophyses (belonging to vertebrae 13-15) remain attached to the third, fourth, and fifth neurals in the type and to the first and fourth neurals of P27372. The first neural gave attachment to two vertebrae, the ninth and tenth, as, for example, in the living *P. expansa*. The upper ends of the spinous processes of these vertebrae are preserved and appear firmly fused to the neural plate, permitting a few details to be given. The spinous process of the ninth vertebra is small and oval in cross section. Its place of fusion with the neural is separated from that of the tenth vertebra by a saddle-shaped, sagittal elevation on the ventral surface of the plate (figs. 6, 7, 8). The spinous process of the tenth vertebra is long and narrow in cross section; its area of fusion with the neural amounts to about 77 per cent of the length of this bone and extends backward to the hind margin of the latter. In *P. expansa* the antero-posterior extent of the attachment of the equivalent spinous process does not reach the posterior margin of the neural and amounts to only about 32 per cent of its length (figs. 6, 7, 8). In *P. barberi* the areas of fusion of the ninth and tenth spinous processes are so close together as to form one attachment scar. It cannot be made out with certainty whether the tenth spinous process in this species reached the posterior end of the neural plate or was short as in *P. expansa*, although the present state of preservation favors the latter interpretation.

The length of the spinous processes of the other vertebrae preserved corresponds both in *P. barberi* and *P. alabamae* to the length of their respective

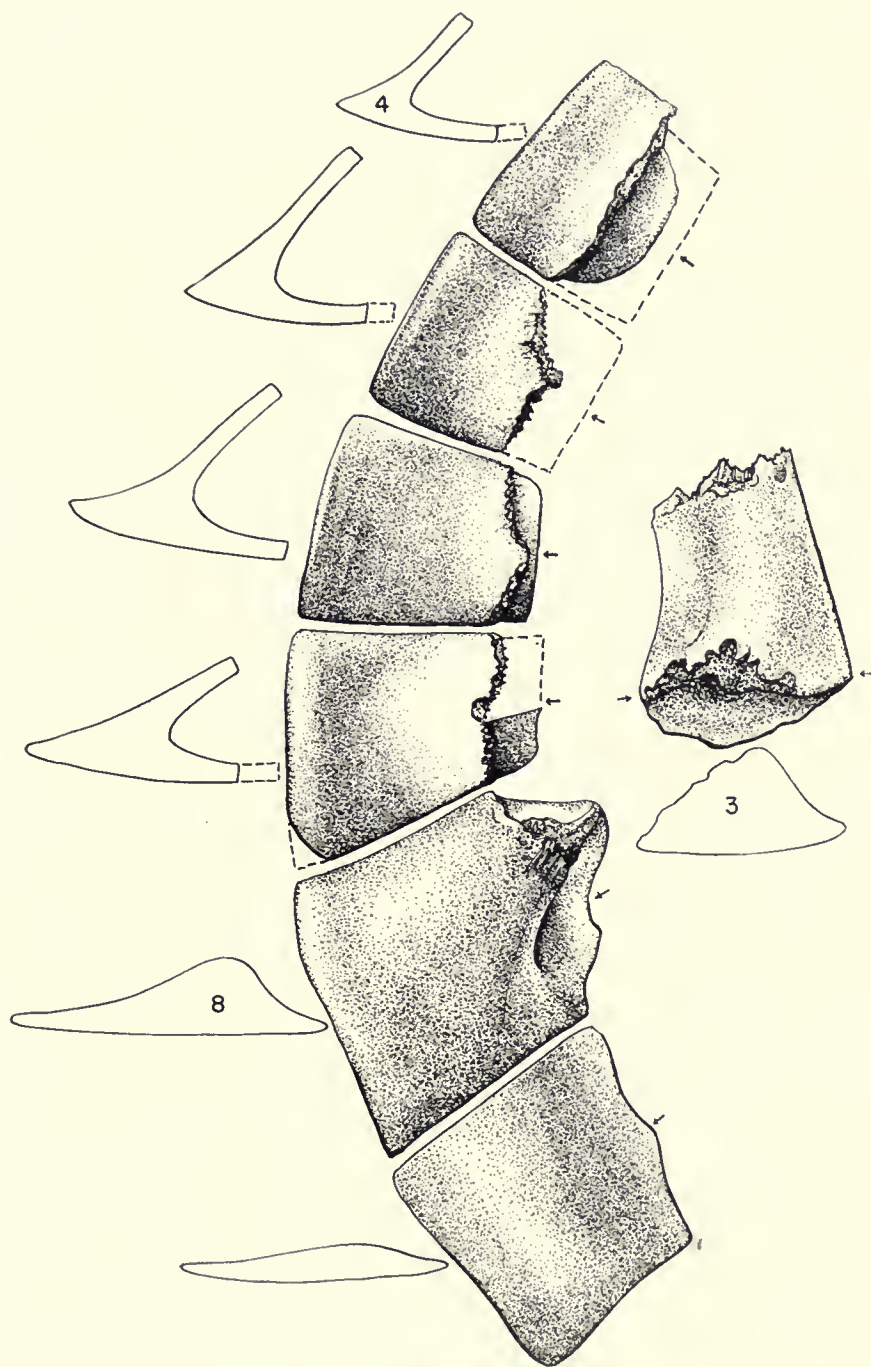


FIG. 4. Third left and fourth to ninth right peripheral plates of *Podocnemis alabamae*, C.N.H.M. P27372. Bones seen in ventral aspect; cross sections indicated by arrows.

neural bones, whereas, in *P. expansa*, the spinous process of the eleventh vertebra is only about half as long as the second neural, that of the twelfth vertebra a little more than half as long as the third neural, and the following two about three-fourths of the length of the fourth and fifth neurals, respectively. The spinous processes are thin fore and aft and very low, as in all observed members of the genus. Just back of mid-length the neurapophyses form strong diapophyseal processes, which, together with the parapophyseal processes of the centra, articulate with the free rib-heads. The dorsal portion of the neural canal is well preserved in the neurapophyses belonging to vertebrae 13 and 14. It is only 4 mm. wide and a delicate crest runs lengthwise in the mid-dorsal line of the canal.

The suprapygal plate is essentially complete in P27369. It is triangular as in *P. barberi*, but is relatively smaller and narrower than in that species.

The costal plates compare very closely with those of *P. barberi*. The buttresses are located below the first and fifth costals, and the three plates between them are narrow for their length. Costal 3 is fairly straight in the plane of the carapace, costal 2 is concave anteriorly and costals 4 to 6 are convex anteriorly (fig. 3; pl. 4, fig. 1). The structures on the visceral surfaces of these plates are well preserved in the type specimen and in P27372 and call for description, particularly since the corresponding surfaces in the type of *P. barberi* are considerably weathered. The buttresses are unequal in size, the axillary one being the stronger. The latter is attached to the entire lateral half of the first costal plate and distinctly lies in the path of the second carapacial rib. The inguinal (hypoplastral) buttress occupies only the outer third of the fifth costal. As is usual in the genus *Podocnemis* (as far as could be observed), the first and second carapacial ribs are thoroughly fused with the first costal plate. In *P. alabamae* the first and second ribs are, at least near their proximal ends, of equal size. In *P. barberi* the first rib slightly exceeds the second in strength, while in *P. expansa* the first rib is distinctly smaller than the second.

The sacral region (figs. 6, 9) is particularly interesting. The state of preservation in the type specimen of *P. barberi* leaves much to be desired, but P27370, P27372, and P27331 from Alabama permit an accurate interpretation of the preserved elements of this relatively complicated area if they are compared to the equivalent structures of a modern form. In a medium-sized specimen of the recent *P. expansa* (pl. 4, fig. 3) the morphology of the sacral region of the shell is as follows: Four vertebrae, numbers 16 to 19, should be considered as sacral vertebrae as their ribs take part in the sacral attachment of the ilium. The ribs of the sixteenth vertebra underlie the seventh costal plate, those of vertebrae 17, 18, and 19 underlie the eighth costal. The ribs of vertebra 17 are thoroughly fused with the eighth costal plates, and the distal ends of the small eighteenth and nineteenth pairs of ribs are fused together, but not with the costal plates. The upper ends of the ilia are joined by suture mainly to the eighth costal pair, and, dorso-medially, to the four pairs of ribs just described. If the ilia become detached by maceration, the areas of their sutural connection with the carapace remain well marked by rough scars (pl. 4, fig. 3). The neurapophy-

ses of the sacral vertebrae, lying behind the last neural plate, are attached by coarse sutures to the medial margins of the sixth and seventh costal bones. In those specimens that have a seventh neural plate, the neurapophysis of the first sacral vertebra (the sixteenth in the series) is attached to it. This is shown by P27405, in which the scar extends the full length of the neural and is 5 mm. wide at mid-length. The last sacral vertebra is free from the carapace. The above description applies essentially to the condition in *P. alabamæ* (fig. 6) where, in the type specimen, the distal ends of the four pairs of sacral ribs and the dorsal end of the right ilium are exceptionally well preserved. The carapacial areas covered by the iliac scars differ greatly in *P. barberi* and *P. alabamæ* on the one hand and the available specimen of *P. expansa* on the other. This difference is due to the difference in shape and extent of the eighth pair of costals and the suprapygal. The narrow suprapygal and the great lateral extent of the eighth costal plates in this specimen of *P. expansa* (pl. 4, fig. 3) seem to be an individual variation that does not reflect the basic podocnemid pattern. An X-ray photograph of a juvenile *P. unifilis* reveals the shapes of the bones in question to be very nearly as in the fossil form here described. In *P. alabamæ* the iliac scars extend laterally onto the seventh costal plates and postero-medially onto the suprapygal for a short distance. The peripherals are adequately illustrated in figures 4 and 5. In the type specimen the bridge peripherals form a sharp lateral edge, but this is probably due to intense dorso-ventral crushing.

Shield furrows are visible on the carapace bones of specimens P27370, P27372, and P27331, but not even an indication of them can be found on the carapace of P27369. Numerically, the scale pattern is identical with that of *P. barberi*. Comparison of the shape of the various scales in these two species is complicated by the well-known fact that the shape of the shields changes with age. Thus, in order to arrive at a conclusion as to whether the shapes of the scutes are the same or not, individuals of approximately the same age or size should be available. This is not the case. P27370 is noticeably smaller than the type of *P. barberi*, and P27369, which is but slightly smaller, lacks any shield impressions. In P27370, as would be expected, the vertebral shields are relatively wider and shorter than in *P. barberi*. In the two smaller specimens from Alabama these scales, in agreement with the rule, are exceedingly short and broad. This is particularly noticeable in P27331, where the fourth vertebral shield is relatively wider than in P27370 (see measurements, p. 38). If the rate of change in the vertebral scale proportions during growth from relatively wide and short to relatively long and narrow remains the same in these forms, then there would be no difference in this respect between *P. alabamæ* and *P. barberi*, and the apparent difference in shape would merely reflect a difference in age. But it appears unlikely that the scale shape changes as much in large individuals as it does in juvenile ones. Until the contrary has been proved, it is better to consider the scale proportions of the two forms as different. The question cannot be definitely answered, however, on the basis of the materials now avail-

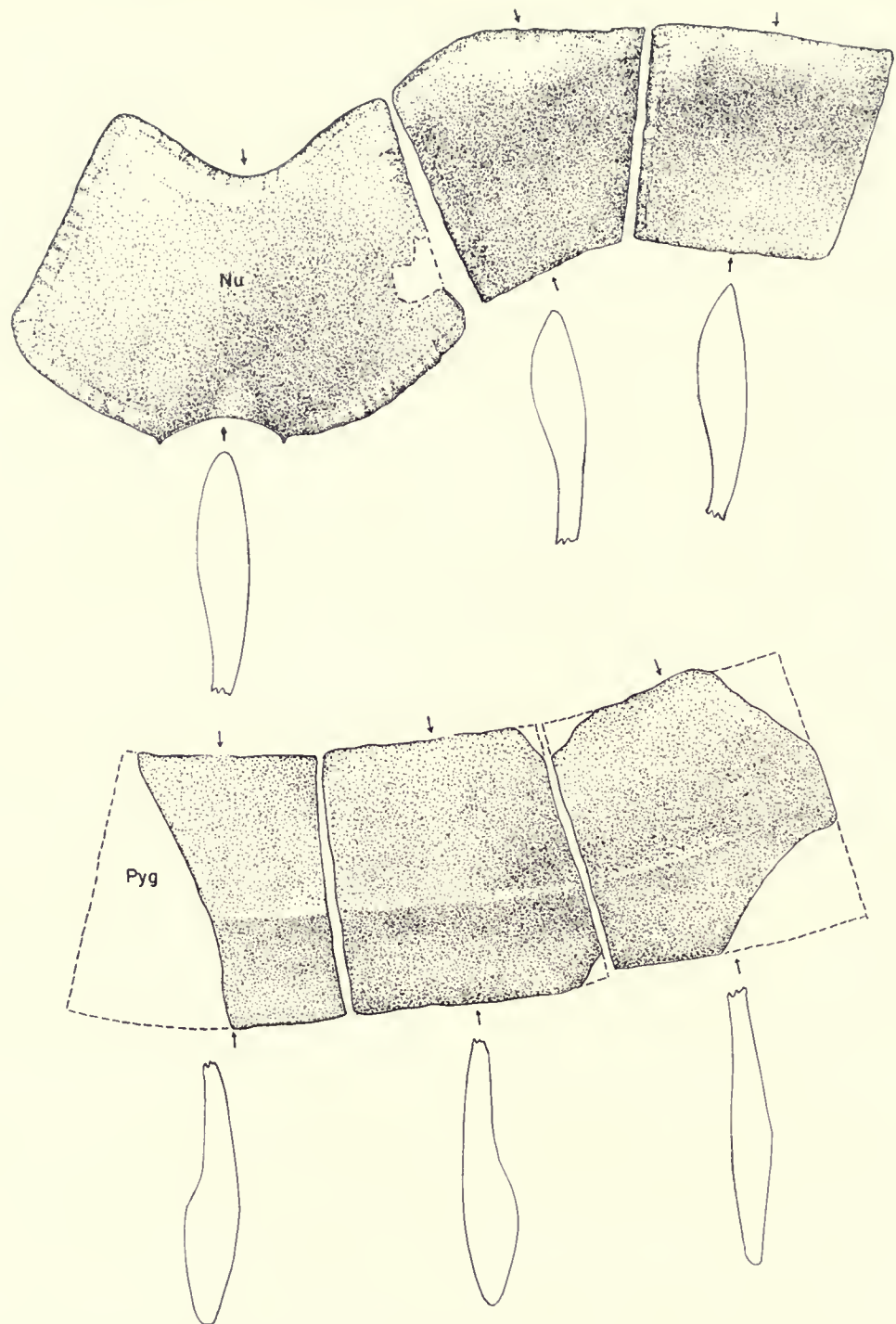


FIG. 5. The nuchal plate with adjoining first and second peripheral bones and the pygal with adjoining eleventh and tenth peripherals of *Podocnemis alabamiae*, C.N.H.M. P27370 (holotype). All bones shown in ventral aspect; cross sections indicated by arrows.

able for study. A slight difference in the position of some of the scale furrows exists between P27370 and P27372. In the latter specimen the posterior margin of the fourth vertebral shield and the anterior third of the sulcus between the fourth costal scute and the fifth vertebral lie on the seventh pair of costal plates, as in *P. barberi*; in the type specimen these furrows lie on the eighth pair of costal bones. In *P. alabamiae* the lateral edges of the first vertebral scale are almost straight (pl. 4, fig. 1), whereas in *P. barberi* they are strongly indented. Irregularities in the scale pattern appear to be fairly common in the Alabama species. In the type specimen there is such an irregularity in the region of the right bridge. The eighth peripheral bone shows on its posterior half the shield furrow in its proper position, but in the anterior portion of the bone it divides to outline a scale that is not normally present in that position. No imprints are visible on the preceding peripheral bone, so that the full extent of the irregularity cannot be made out. In P27372 a similar accessory scute lay between the peripheral and costal shields on the left side of the shell on peripheral 6 and presumably on peripheral 7, which is lacking.

There is little evidence of pathological deformations, except in the carapace of P27372. The anterior point of the right first costal plate is greatly deformed, probably as a result of a parasitic infestation (fig. 7). The adjoining first and second peripheral bones are missing, so that the full extent of the injury cannot be determined. There are three deep, oblong depressions cut into the dorsal surface of the costal; anteriorly they merge to form what appears to be a large hole piercing the plate completely. As the erosion grew deeper, bone was deposited on the visceral side of the plate, thus forming a large, somewhat irregular nodule. Similar phenomena can sometimes be observed on shells of modern turtles, for example, in a specimen of *Pelusios sinuatus*, C.N.H.M. 12699. The formation of bone on the inside of plates that are beset with parasitic erosions on the outer surface, is not a very common occurrence. Normally the shell simply becomes pierced. Two such holes penetrate the shell of P27372, one between the left tenth and eleventh peripherals and the other between the fourth and fifth costals.

Plastron

The general shape of the plastron is very similar to that of *P. barberi*. The anterior lobe is short and broadly rounded, and the posterior lobe is about as wide as long, with the xiphiplastral end deeply notched (fig. 11; pl. 4, fig. 2). The plastron is thickest near the midline at the level of the inguinal buttresses. The anterior edge of the epiplastron is blunt, in contrast to *P. barberi*, where it is acute. In P27369, where no sign of crushing is visible, the epiplastra form swollen lips on either side of the median line and the edge between these lips is straight (pl. 4, fig. 2). These details are not so well shown in the type specimen because the epiplastra have been compressed dorso-ventrally. The remaining plastral elements are much as in *P. barberi*, but the mesoplastron is slightly wider transversely in the Alabama form. As in *P. barberi*, both the ischial and

the pubic scars on the xiphiplastra are elevated and coarse. The ischial scars do not extend quite to the midline (fig. 11). The plastral shield sulci are present neither in the type of *P. barberi* nor in that of *P. alabamæ*, but in P27369 they are clearly discernible. As in the modern South American species, for example, *P. expansa*, there are the usual six pairs of plastral scutes plus an unpaired intergular shield. The general arrangement of the pattern is very similar to that of *P. expansa*; the intergular and gular shields are relatively shorter in *P. alabamæ* and the pectoro-abdominal furrows cross onto the mesoplastra in the latter, but not in the former species. In *P. expansa* the hypo-xiphiplastral sutures lie, laterally, about halfway between the abdomino-femoral and the femoro-anal sulci; in *P. alabamæ* they are distinctly closer to the femoro-anal furrows (fig. 3).

The inner surface of the preserved portion of the entoplastron of P27370, instead of being flat as in other specimens, seems to have formed a strong boss or a sagittal crest that has become intensified by crushing. The entoplastron of P27369 is longer than wide as seen from the visceral surface, wider than long on the outer surface (fig. 3; pl. 4, fig. 2), a difference due to growth. The suture between the entoplastron and the hyoplastra is nearly vertical in young individuals, but, as the shell becomes larger, the entoplastron grows in length faster on the inside than on the outside. Consequently, the angle between the suture and the plane of the plastron becomes smaller.

Shoulder Girdle and Humerus

Of the shoulder girdle only parts of the scapulae are known; these are similar to equivalent parts in *P. expansa*, but a detailed comparison cannot be made.

A right humerus found with P27405 is of particular interest. The over-all length of the bone is 97.5 mm. The shaft is curved, as in *P. expansa*, but instead of an entepicondylar foramen there is a shallow, distinct groove (fig. 13). The relative sizes of the caput humeri and the radial and the ulnar processes are similar to those of *P. expansa*. In the latter there is, on the ventral side, a broadly V-shaped ridge connecting the radial and ulnar processes. This ridge is not developed in *P. alabamæ*. On the ventral face of the shaft, a moderately acute ridge, originating at the base of the ulnar process, runs toward the distal end of the humerus. In *P. expansa* it runs approximately parallel with the shaft; in *P. alabamæ* it crosses over to the radial side and ends below the entepicondylar groove (fig. 13). Probably because of the differences in the region of the entepicondylar canal, the humerus is relatively narrower at its distal end than in *P. expansa*.

Pelvis

The dorsal part of the ilium is shown in figure 6. It corresponds fairly well to the corresponding part in *P. expansa*, but the depression on the antero-medial face of the bone is much deeper in the Alabama form. The right ischium and pubis are illustrated in figure 12. Their sutural ventral ends fit well into the corresponding scars on the xiphiplastron. The height of these bones is about

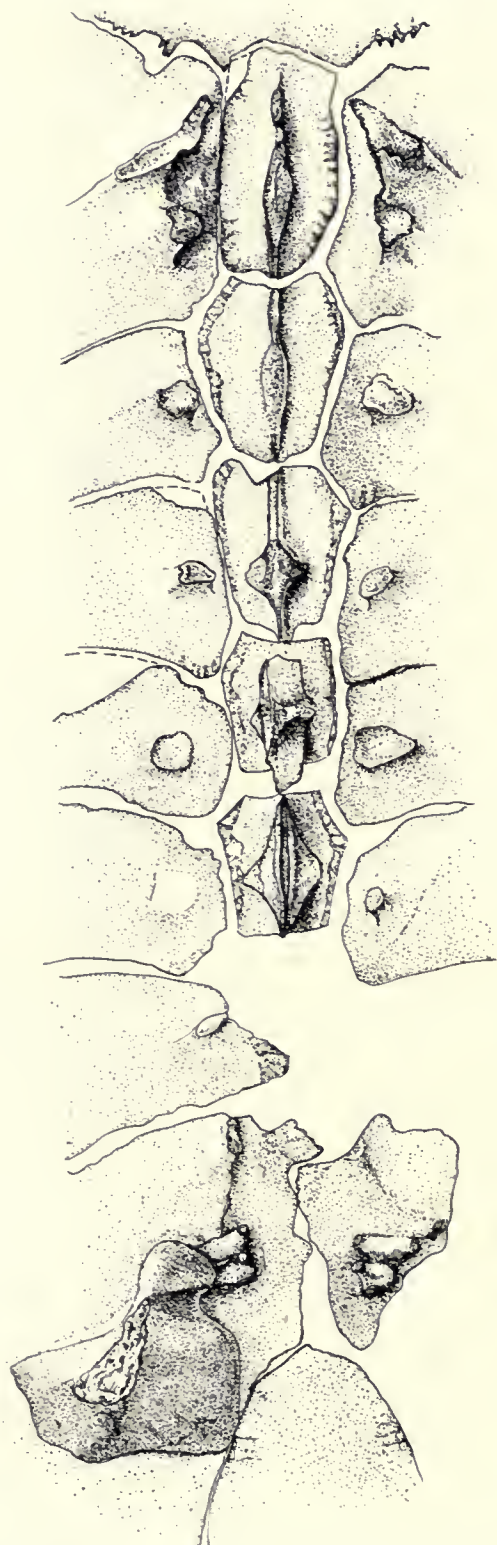


FIG. 6. Ventral aspect of middle part of carapace of *Podocnemis alabamiae*, C.N.H.M. P27370 (holotype). Dorsal end of ilium and several neurapophyses preserved in situ (cf. pl. 4, fig. 1).

50 mm. They resemble closely those of *P. expansa*, but their state of preservation does not justify close comparison.

Measurements

In the table below, the actual measurements of the type and referred specimens of *P. alabamiae* and of the type of *P. barberi* are listed, together with their relative values calculated according to the following formula:

$$\frac{\text{Measurement of character} \times 100}{\text{Maximum width of nuchal plate}^1}$$

The figures indicate rather clearly that the over-all geometric patterns of the Alabama specimen P27369 and the type of *P. barberi* (the two individuals are most nearly of the same size) are very similar. The indices worked out for the type of *P. alabamiae* (P27370) and the much smaller individual (P27372) do not fit as well into the pattern of P27369 or into that of *P. barberi*.

Three factors, at least, are responsible for the irregular index pattern of the more complete specimens of *P. alabamiae*: individual variation, differences in age of the members of the sample, and an undeterminable amount of distortion that not only affects each specimen in different degrees but also the various parts of each specimen. If, the amount of variation in a uniform sample of a living species of *Podocnemis* were known, together with the proportional changes that take place during growth, it would be possible, by analogy, to properly evaluate the present material and to determine approximately the degree of

¹ This measurement was used because it could be obtained accurately in the better-preserved specimens.

MEASUREMENTS

	MEASUREMENTS					<i>barberi</i> P26055	INDICES					<i>barberi</i> P26055
	<i>alabamiae</i>						<i>alabamiae</i>					
	P27369	P27370	P27372	P27331			P27369	P27370	P27372	P27331		
Length of carapace (tape).....	582	520		654	489.0	440.6		491.7
Width of carapace (tape).....	607	597	390		682	510.0	505.9	481.4		512.7
Length of nuchal plate.....	77	60		87	64.7	50.8		65.4
Length of neural plates												
First.....	64	57	35		64	53.7	48.3	43.2		48.1
Second.....	47	39	±27		51	39.4	33.0	33.3		38.3
Third.....	48	46	±34		57	40.3	38.9	41.9		42.8
Fourth.....	39	35	31		49	32.7	29.6	38.2		36.8
Fifth.....	41	33	±26		49	34.4	27.9	32.0		36.8
Sixth.....	34	±32	±24		39	28.5	27.1	29.6		29.3
Seventh.....	26	21.8
Length of suprapygal plate.....	63	49	±33		77	52.9	60.4		57.8
Length of pygal plate.....	±78	62		91	65.5	52.5		68.4
Anterior width of nuchal plate.....	55	61		54.5	46.2	51.6		40.9
Anterior width of neural plates												
First.....	38	31	22		43	31.9	26.2	27.1		32.3
Second.....	31	23	?18		30.5	26.0	19.4	22.2		22.9
Third.....	30	19	?19		24	25.2	16.1	23.4		18.0
Fourth.....	24	19	15		23	20.1	16.1	18.5		17.2
Fifth.....	±27	21	14		25	22.6	17.7	17.2		18.7
Sixth.....	28	22		25	23.5	18.6		18.7
Seventh.....	20	16.8
Anterior width of pygal plate.....	±48	±44		49	40.3	37.2		36.8
Posterior width of suprapygal.....	83	72	64	±47		106	69.7	61.0	79.0		79.6
Posterior width of pygal.....	±89	±68		92	74.7	57.6		69.1
Maximum width of nuchal plate.....	119	118	81		133	100.0	100.0	100.0		100.0
Maximum width of neural plates												
First.....	45	40	29		50	37.8	33.8	35.8		37.5
Second.....	51	38	±30		51	42.8	32.2	37.0		38.3
Third.....	48	36	±30		47	40.3	30.5	37.0		35.3
Fourth.....	±41	33	27		42.5	34.4	27.9	33.3		31.9
Fifth.....	±47	37	±29		45	39.4	31.3	35.8		33.8
Sixth.....	46	±42	±30		42	38.6	35.5	35.8		31.5
Seventh.....	±33	27.7

MEASUREMENTS—continued

	MEASUREMENTS					barberi P26055	INDICES					barberi P26055
	alabamæ						alabamæ					
	P27369	P27370	P27372	P27372	P27331		P27369	P27370	P27372	P27331		
Anterior height of first peripheral.....	66	58	87	55.4	49.1	65.4	
Posterior height of peripherals												
First.....	67	44	65	56.3	37.2	48.8	
Second.....	65	44	29	56	54.6	37.2	42.1	
Third.....	69	±47	32	57	57.9	39.8	42.8	
Fourth.....	±60	39	74	50.8	55.6	
Fifth.....	69/63	46	84.5	55.9	63.5	
Sixth.....	775	49	102	63.5	76.6	
Seventh.....	52	105	78.9	
Eighth.....	91	775	49	109	76.4	63.5	81.9	
Ninth.....	69	771	38	90	57.9	60.1	67.6	
Tenth.....	65	756	734	71	54.6	47.4	53.3	
Eleventh.....	69	756	734	78	57.9	47.4	58.6	
Inner length of peripherals												
First.....	30	32	25	25.2	27.1	18.8	
Second.....	49	756	51	41.1	47.4	38.3	
Third.....	68	762	50	78	57.1	52.5	58.6	
Fourth.....	69	40	31	58	57.9	33.8	43.6	
Fifth.....	43/45	31	54	37.2	40.6	
Sixth.....	46	35	56	38.9	42.1	
Seventh.....	731	54	40.6	
Eighth.....	70	45	78	59.3	58.6	
Ninth.....	66/70	67	51	90	57.1	56.7	67.6	
Tenth.....	53	58	41	70	44.5	49.1	52.6	
Eleventh.....	50	50	35	60	42.0	42.3	45.1	
Outer length of peripherals												
First.....	59	67	72	49.5	56.7	54.1	
Second.....	75	59	77	63.0	50.0	57.8	
Third.....	±82	66	49	78	68.9	55.9	58.6	
Fourth.....	58	45	76	49.1	57.1	
Fifth.....	77	56	40	77	64.7	47.4	57.9	
Sixth.....	76	63	41	75	63.8	53.3	56.4	
Seventh.....	78	65	48	82	65.5	55.0	61.6	
Eighth.....	84	779	55	97	70.5	66.9	72.9	
Ninth.....	70	779	55	91	58.8	66.9	68.4	
Tenth.....	56	762	±44	87	47.0	52.5	65.4	
Eleventh.....	64	60	41	78	53.7	50.8	58.6	

MEASUREMENTS—concluded

	MEASUREMENTS						INDICES			
	alabamiae						alabamiae			
	P27369	P27370	P27372	P27331	barberi	P26055	P27369	P27370	P27372	P27331
Plastron										
Length in sagittal plane.....	379	±300	498		318.4	254.2
Width anterior to bridge.....	280	?260	180	320		235.2	220.3
Width posterior to bridge.....	240	220	285		201.6	186.4
Length of anterior lobe.....	120	±100	120		100.8	84.7
Length of posterior lobe.....	160	±160	190		134.4	135.5
Length of epiplastral symphysis.....	25	20	31		21.0	16.9
Length of entoplastron.....	81	41	±70		68.0
Length of hypoplastral symphysis.....	±120	120/110*	134/126*		100.8	97.4
Length of hypoplastral symphysis.....	±120	90/95*	75/80*	132/119*		100.8	78.3
Length of xiphiplastral symphysis.....	130	100/110*	136/154*		109.2	88.9
Length of posterior wings.....	40	44		33.6
Width of entoplastron.....	103.5	78	41	90		86.9	66.1
Length of hyo-hypoplastral suture.....	130	125	89	144		109.2	105.9
Width of mesoplastron.....	±82	?72.5	46	81		68.9	61.4
Length of mesoplastron.....	±71	?51	39	66		59.6	43.2
Distance between posterior wings.....	108	?100	±97		90.7	84.7
Scales										
Maximum width, second vertebral shield.....	119	106	128		100.8	130.8
Maximum width, third vertebral shield.....	127	107	123		107.6	132.0
Maximum width, fourth vertebral shield.....	130	114	75.5	129		110.1	140.0
Anterior width, first vertebral shield.....	117	129		99.1
Anterior width, second vertebral shield.....	53	37.5	78		44.9	46.2
Anterior width, third vertebral shield.....	75	±58	85		63.5	71.6
Anterior width, fourth vertebral shield.....	79	±56	36	85		66.9	69.1	70.5
Anterior width, fifth vertebral shield.....	44	35	27	52		37.3	43.2	52.9
Posterior width, fifth vertebral shield.....	?140	118	78	±216		118.6	145.0	152.9
Length of nuchal shield.....	12	18		10.1
Length of first vertebral shield.....	79	103		66.9
Length of second vertebral shield.....	90	±60	111		76.2	74.0
Length of third vertebral shield.....	79	±61	106		66.9	75.3
Length of fourth vertebral shield.....	90	±63	37.5	108		76.2	77.7	73.5
Length of fifth vertebral shield.....	?119	71	152		100.8	87.6

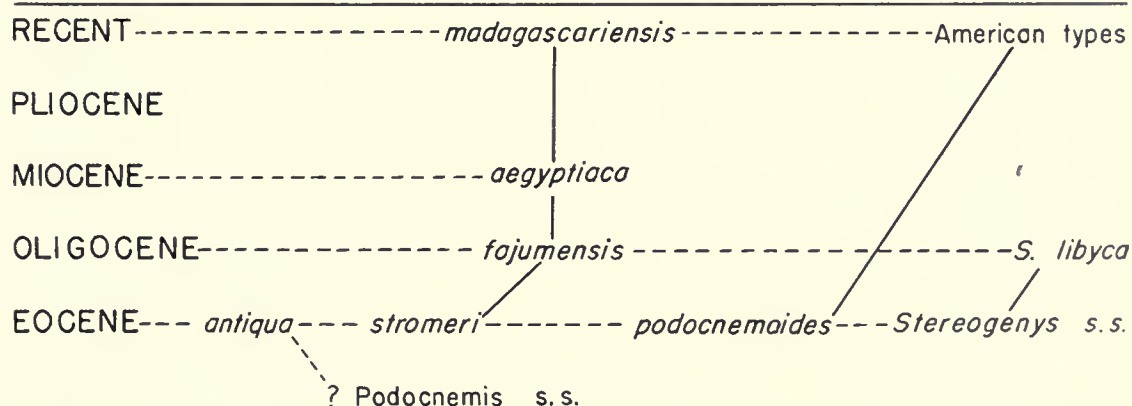
* Left/right.

distortion suffered by the fossils. To my knowledge, however, such information is not available at present. In order to make statistical treatment possible at a later date, the complete set of measurements is herewith published.

Systematic Relationships

Fossil turtles definitely referable to the Pelomedusidae were first found in the London Clay and described by Owen and Bell (1849), but it is doubtful that these forms belong to any of the living genera. In the early part of this century, however, a number of fossil representatives of all three living genera of the family were discovered in Egypt and described by Andrews (1900, 1901, 1903, and 1906) and von Reinach (1903).

Dacqué (1912) published an excellent review of the fossil turtles of the Tertiary of Egypt and attempted an outline of the phylogenetic relationships that appeared to exist between the fossil Egyptian pleurodiran turtles and the living forms. Since much of the fossil turtle material from Egypt belongs to the existing *Podocnemis* and to the related, extinct *Stereogenys*, a discussion of the probable relationships of these fossils to the Recent species of *Podocnemis* was of necessity included as of particular interest in view of the striking discontinuous distribution of the latter in northern South America and in Madagascar. At that time no fossil representatives of the genus *Podocnemis* were known from the New World. Dacqué, obviously with reservations in his mind (he points out the fact that no fossil American species had yet been described), assumed that the genus had originated in the Old World, particularly in the region of Egypt. In late Eocene beds of this area there were thus known to occur species definitely belonging to *Podocnemis* (*P. stromeri* von Reinach, *P. antiqua* Andrews) as well as two species belonging to the closely related *Stereogenys* (*S. cromeri* Andrews and *S. podocnemoides* von Reinach). Both genera were also



known from Oligocene deposits (*P. fajumensis* Andrews and *S. libyca* Andrews). *P. aegyptiaca* Andrews had been recorded from beds of Miocene age.

Dacqué clearly recognized that all of these species of *Podocnemis* were closer morphologically to the living *P. madagascariensis* than to the New World forms. This interpretation was based chiefly on the scale pattern of the anterior plastral

lobe. In *P. madagascariensis*, the intergular shield is small and triangular; both the gular and humeral scales meet at the midline. In the New World species the intergular is noticeably larger and the gular shields do not meet in the sagittal plane, but are more or less small, triangular scales on either side of the intergular. The diagram (p. 39) illustrates the morphological affinities of the extinct Egyptian and the living species according to Dacqué's interpretation (1912, p. 13). He derived the various forms from a morphological type (called by him *Podocnemis* s.s.) in which the scale pattern of the anterior plastral lobe was considered to be essentially that of the living Madagascar species. From this morphological type, *Podocnemis stromeri* was derived by a displacement of the gulo-humeral sulci forward to the posterior tip of the intergular. The *fajumensis-aegyptiaca-madagascariensis* type results from the *stromeri*-pattern by diminution of the intergular shield. In *Stereogenys podocnemoides*, the intergular shield is relatively large, the gulars are relatively small, triangular scales, and the posterior tips of the humeral scutes meet at the hind end of the intergular (fig. 15, B). By decrease in length of the intergular, the pattern of the living South American species of *Podocnemis* could be arrived at (fig. 15, L). An additional forward displacement of the humero-pectoral sulcus would lead to the *Stereogenys* s.s. pattern (fig. 15, C).

Dacqué regarded *Pelusios* as a morphological derivative from the line leading from *Stereogenys podocnemoides* to the living South American *Podocnemis* spp.¹

The discovery of representatives of *Podocnemis* in the late Cretaceous of both North and South America,² reopens the question of relationships among the various pelomedusid pleurodires. It is now obviously no longer possible to derive the recent South American species from an Old World form such as *Stereogenys podocnemoides*; a restudy of the morphological affinities of the members of the genus *Podocnemis* and of the Pelomedusidae as well is necessary.

The modern pleurodiran turtles fall readily into two groups, the Pelomedusidae and the Chelyidae. Of these families the former includes the more generalized living pleurodires, *Pelusios* Wagler, *Pelomedusa* Wagler, and *Podocnemis* Wagler. The plastron includes mesoplastral elements; these either meet at the midline and separate the hyoplastral and hypoplastral plates entirely (*Pelusios*), or are small, more or less circular plates, laterally wedged between the hyo- and hypoplastra (*Pelomedusa* and *Podocnemis*; fig. 14). In *Pelusios* the anterior lobe of the plastron is movable, a hinge being present between the hyo- and mesoplastra (fig. 14, B). In the carapace there is always a series of neural plates varying from eight to six in number. In the Chelyidae mesoplastral bones are absent and there is a distinct tendency toward reduction of the neuralia. In

¹ This view is, in my opinion, quite untenable, since *Pelusios* has large mesoplastral plates (fig. 14, B) that meet in the midline, much as in the Pleurosternidae, for example, *Glyptops*, a condition here considered as primitive in view of its general occurrence among the phylogenetically older Amphichelydia.

² Further preparation of the type and only known specimen of *Podocnemis olssoni* Schmidt from the Eocene of Peru (Schmidt, 1931) revealed that this species does not belong to *Podocnemis*, but to the genus *Taphrosphys* (fig. 15, F), so far known mainly from the Green Sand deposits of New Jersey. A redescription of this specimen was recently published (Zangerl, 1947).

Rhinemys there are but four neurals; in *Chelodina oblonga*, *Platemys platycephala*, and *Emydura macquariae* neural plates are totally lacking.

Among the fossil turtles there are a number of forms that can definitely be assigned to the family Pelomedusidae. All three of the modern genera are represented in the fossil record, and, in addition, the genera *Stereogenys* Andrews from the Tertiary of Egypt and *Taphrosphys* Cope from New Jersey and Peru (see above) must on the basis of present knowledge be included in the family. *Amblypeza* Hay is poorly known. It is close to *Taphrosphys*, from which it may not be generically distinct. *Naiadochelys* Hay is based on a small xiphiplastral fragment, and the Patagonian materials referred to this genus by Staesche (1929) on what appear to me to be very uncertain grounds scarcely add to the knowledge of this form. The meager fragments, however, indicate a turtle close to *Podocnemis*. The recognized genera and species of the Pelomedusidae stand as follows:

Family PELOMEDUSIDAE

Genus *Pelusios* Wagler

<i>P. niger</i> Dumeril and Bibron	West Africa	Recent
<i>P. sinuatus</i> Smith	Africa	Recent
<i>P. nigricans</i> Donndorff	Madagascar	Recent
<i>P. derbianus</i> Gray	Africa	Recent
<i>P. adansonii</i> Schweigger	West Africa	Recent
<i>P. gambonensis</i> A. Dumeril	Angola	Recent
<i>P. dewitzianus</i> von Reinach	Egypt	Pliocene
<i>P. blanchenhorni</i> Dacqué	Egypt	Miocene

Genus *Pelomedusa* Wagler

<i>P. galeata</i> Schoepff	Africa, Madagascar	Recent
<i>P. progaleata</i> von Reinach	Egypt	Oligocene

Genus *Platycheloides* Houghton

<i>P. nyasae</i> Houghton	Nyasaland	Age uncertain ?Cretaceous
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Genus *Podocnemis* Wagler

<i>P. cayennensis</i> Schweigger	Northern South America	Recent
<i>P. dumeriliana</i> Schweigger	Northern South America	Recent
<i>P. expansa</i> Schweigger	Northern South America	Recent
<i>P. lewyana</i> Dumeril	Northern South America	Recent
<i>P. sextuberculata</i> Cornalia	Northern South America	Recent
<i>P. unifilis</i> Troschel	Northern South America	Recent
<i>P. vogli</i> Müller	Northern South America	Recent
<i>P. madagascariensis</i> Grandidier	Madagascar	Recent
<i>P. aegyptiaca</i> Andrews	Egypt	Miocene
<i>P. bramlyi</i> Fourtau	Egypt	Miocene
* <i>P. lata</i> Ristori	Malta	Miocene
<i>P. fajumensis</i> Andrews	Egypt	Oligocene
* <i>P. dehmi</i> Bergounioux	Germany	Oligocene
<i>P. antiqua</i> Andrews	Egypt	Eocene
<i>P. stromeri</i> von Reinach	Egypt	Eocene
<i>P. indica</i> Lydekker	India	Eocene
<i>P. bowerbanki</i> Owen and Bell	England	Eocene
* <i>P. congolensis</i> Dollo	Congo	Paleocene
* <i>P. harrisi</i> Pacheco	São Paulo	Late Cretaceous
<i>P. brasiliensis</i> Staesche	São Paulo	Late Cretaceous
<i>P. barberi</i> Schmidt	Arkansas	Late Cretaceous
<i>P. alabamae</i> sp. nov.	Alabama	Late Cretaceous

Genus <i>Stereogenys</i> Andrews		
<i>S. libyca</i> Andrews.....	Egypt	Oligocene
<i>S. cromeri</i> Andrews.....	Egypt	Eocene
<i>S. podocnemoides</i> v. Reinach.....	Egypt	Eocene
Genus <i>Taphrosphys</i> Cope		
* <i>T. sulcatus</i> Leidy.....	New Jersey	?Eocene
<i>T. longinuchus</i> Cope.....	New Jersey	?Eocene
<i>T. leslianus</i> Cope.....	New Jersey	?Eocene
* <i>T. strenuus</i> Cope.....	New Jersey	?Eocene
<i>T. molops</i> Cope.....	New Jersey	?Eocene
* <i>T. dares</i> Hay.....	Not known	Not known
* <i>T. nodosus</i> Cope.....	New Jersey	?Eocene
<i>T. olssoni</i> Schmidt.....	Peru	Eocene
Genus <i>Amblypeza</i> Hay*		
* <i>A. entellus</i> Hay.....	New Jersey	?Eocene
Genus <i>Dacochelys</i> Lydekker*		
<i>D. delabechei</i> Bell.....	England	Eocene
Genus <i>Naiadochelys</i> Hay*		
* <i>N. ingravata</i> Hay.....	?New Mexico	?
* <i>N. patagonica</i> Staesche.....	Patagonia	Late Cretaceous
* <i>N. major</i> Staesche.....	Patagonia	Late Cretaceous
Genus <i>Shweboemys</i> Swinton*		
† <i>S. pilgrimi</i> Swinton.....	Upper Burma	Pliocene

* Poorly known or doubtful genera and species.

† Skull only.

If the pelomedusid plastron is compared to that of the Pleurosternidae, where one pair of mesoplastra, meeting at the midline, is suturally joined to the hyoplastra, and to that of the Baenidae, where the mesoplastra are either completely developed as in the Pleurosternidae, or medially reduced in varying degrees, it becomes clear that the morphological type from which the pelomedusid condition can be derived, is, in principle, that of the pleurosternid plastron. The scale pattern of the pelomedusid plastron presents a much less clear-cut picture, but a few basic features are apparent. The gular shields are almost always separated anteriorly by a relatively large intergular scale. Only in *Taphrosphys molops* Cope does the intergular appear to be displaced caudad so that the gular scutes meet in front of it (essentially as in *Chelodina oblonga* Gray). In *Podocnemis fajumensis*, *P. aegyptiaca*, and *P. madagascariensis* the intergular is small and very narrow (fig. 15, H, I, K). In most Tertiary and Recent species of *Podocnemis* the humero-pectoral sulci meet in the anterior part of the entoplastron; in the Cretaceous species in the posterior half of the entoplastron; in *Pelusios* along the posterior margin of the entoplastron; and in *Pelomedusa*, the Pleurosternidae, and Baenidae far behind the entoplastron. The pectoro-abdominal shield furrows follow the hyo-mesoplastral hinge in *Pelusios*. In *Pelomedusa* they lie close to the hyo-hypoplastral sutures and extend onto the lateral mesoplastra. The same condition prevails in *Podocnemis alabamiae*. In the remaining forms the sulci lie farther forward, bending backward laterally, but do not extend onto the mesoplastra. In the Pleurosternidae and Baenidae they extend

across the mesoplastra. The abdomino-femoral and femoro-anal shield furrows do not exhibit any significant positional relationships in the forms here considered.

These comparisons permit the deduction that the basic plan of organization of the pelomedusid plastron includes a pair of medially joining mesoplastral bones. The intergular shield is relatively large, separating the gular scales. The humero-pectoral sulci lie behind the entoplastron, and the pectoro-abdominal furrows lie on the mesoplastra (fig. 14, A).

The pelomedusid carapace presents a fairly generalized picture. On the whole, it compares favorably with that of the Pleurosternidae and Baenidae.

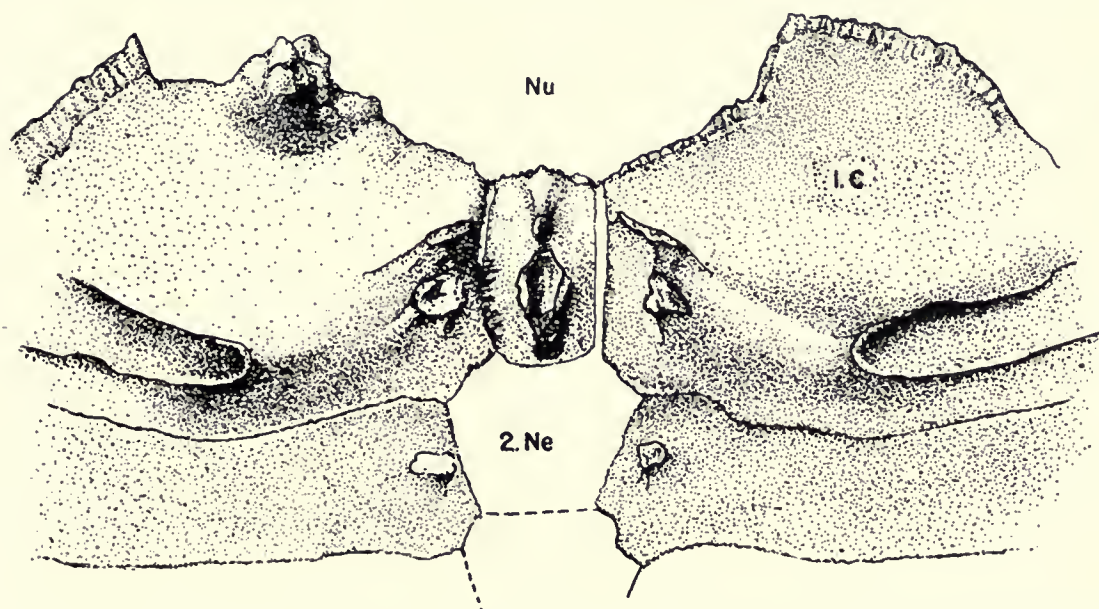


FIG. 7. Ventral aspect of anterior portion of carapace of *Podocnemis alabamæ*, C.N.H.M. P27372. The rugosity at the anterior edge of the right first costal is a parasitic deformation. Nu, nuchal plate (missing); 1c, first costal plate; 2Ne, second neural plate (missing).

The major differences lie in the tendency toward reduction of the neural plates and in the absence of a nuchal scale (except in *Amblypeza*) in the Pelomedusidae. *Pelusios derbianus* has eight neurals, *P. sinuatus* (C.N.H.M. 12699) has six, *Pelomedusa* seven, and *Podocnemis* six or seven. The various Egyptian species of *Podocnemis* as well as the Recent *P. madagascariensis* have six, the living South American species have seven (occasionally there is a specimen with only six, for example, a shell of *P. expansa*, C.N.H.M. 16075), the late Cretaceous *P. barberi* has six, *P. brasiliensis* seven, and *P. alabamæ* six or seven. *Stereogenys* and *Taphrosphys* have seven neurals. In most cases the first neural plate adjoins the nuchal bone, but in *Stereogenys* it appears to be displaced caudad, permitting the first pair of costal plates to join sagittally. This character was observed in several individuals and may be characteristic of the genus.¹ In *Pelomedusa*

¹ The carapace referred to *S. podocnemoides* by von Reinach may not belong to this species. It can scarcely be distinguished from *Podocnemis stromeri* (Dacqu , 1912, p. 24).

galeata the first neural is either a long, slender plate adjoining the nuchal or a small, round plate widely separated from it (C.N.H.M. No. 17160). A condition similar to that of *Stereogenys* thus occurs in this species as an individual variation, but here it is clearly a reduction of the anterior part of the first neural, whereas in *Stereogenys* there seems to be a caudad segmental displacement of neural plates 1 to 5, whereby Nos. 6 and 7 come to occupy the space held by the seventh neural alone in *Podocnemis*. Within the family Pelomedusidae there is a difference in relationship of the first vertebral scute to the first and second marginal

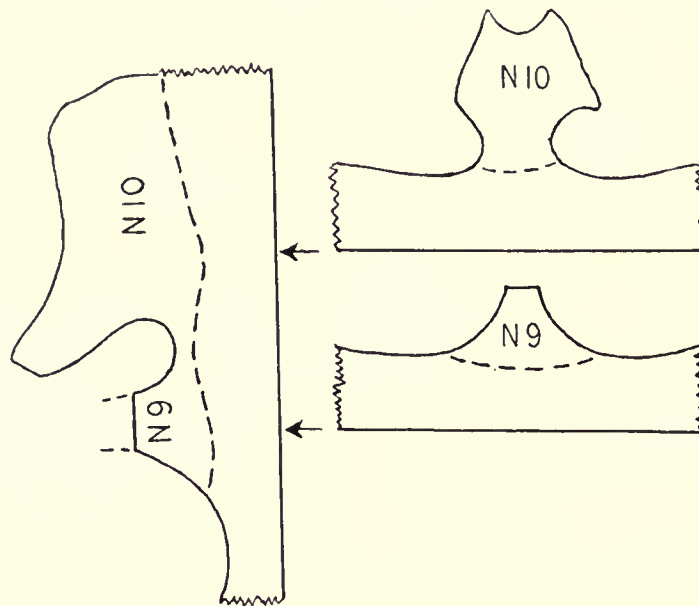


FIG. 8. Longitudinal and cross sections through first neural bone of *Podocnemis alabamae*, with parts of neurapophyses of vertebrae Nos. 9 and 10 attached. C.N.H.M. P27372.

scales. In the living species of *Podocnemis* and in *Stereogenys* the lateral shield furrow of the first vertebral ends at the first marginal scale; in all other pelomedusid turtles it ends at the second marginal. In the Pleurosternidae with a wide nuchal scale, for example, *Glyptops*, the furrow in question ends at the first marginal scute. In the Baenidae this region is exceedingly variable.

The morphological type of the pelomedusid carapace can be characterized as follows: It greatly resembles that of the Pleurosternidae, with eight neural plates, the first adjoining the nuchal bone. There is no nuchal shield and the lateral shield furrows of the first vertebral end at the second marginal scales (fig. 14, A).

The attempt may now be made to establish the morphological affinities between the various pelomedusid turtles with regard to the mutual structural plan of the shell, and based on those features that have been discussed.

If the basic type pattern of the pelomedusid shell (fig. 14, A), arrived at above, is compared with the actual representatives of the family it becomes clear that the latter fall into two major groups, one represented by *Pelusios*, the other

by *Podocnemis*, *Pelomedusa*, *Stereogenys*, and *Taphrosphys*. The two groups are considered as subfamilies, Pelusiinae and Pelomedusinae, diagnosed on page 48. In the Pelusiinae (fig. 14, B) the sutural union of the hyoplastron with the mesoplastron is replaced by a hinge, the pectoro-abdominal sulci run next to the hinge, the humero-pectoral furrows are farther anterior, being situated at the hind margin of the entoplastron, and the intergular and gular shields are smaller than in the morphological type. In the Pelomedusinae (fig. 14, C) the medial portions of the mesoplastra are reduced; the pectoro-abdominal scale lines lie

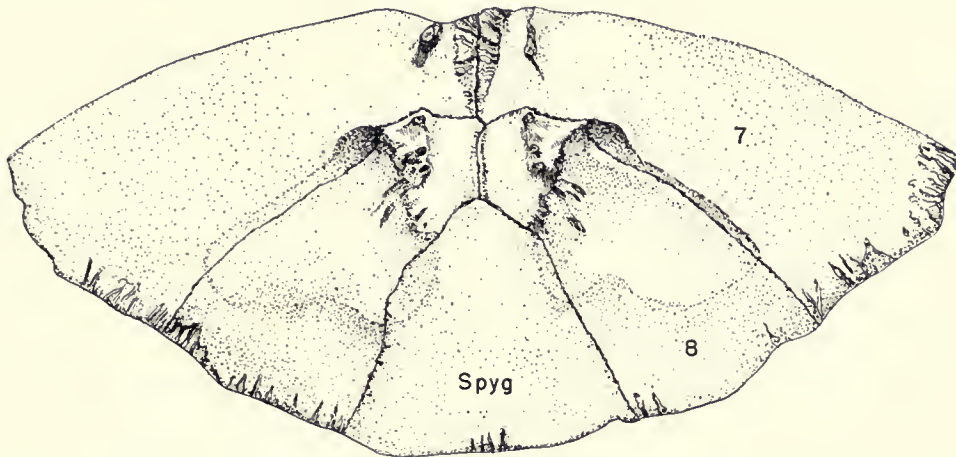


FIG. 9. Ventral view of posterior portion of carapace of *Podocnemis alabamiae*, C.N.H.M. P27372, showing extent of ilial attachment scar, sacral rib stubs on costal plates 8 and neurapophyseal rugosity along medial edges of costal plates 7 (cf. pl. 4, fig. 3).

farther forward, laterally transgressing onto the mesoplastra; the intergular is large, more or less triangular; and the gular shields are relatively smaller than in the family type pattern. In the carapace the neural series is reduced to seven plates.

Podocnemis, *Pelomedusa*, *Stereogenys*, and *Taphrosphys* can be morphologically derived from the pelomedusine type pattern (figs. 14, C, and 15, A).

Stereogenys can be derived from the pelomedusine pattern by diminution of the humeral scutes so that they become totally separated by the intergular, as in *S. podocnemoides*. A further diminution of the humeral shields leads to the condition in *Stereogenys cromeri* Andrews where the posterior point of the intergular partially separates the pectoral scutes. A decrease in size of all the anterior plastral shields leads in turn to *S. libyca* Andrews. In the carapace, the caudad displacement of neural plates 1 to 5 is combined with a very narrow first vertebral scale. *Taphrosphys* is a parallel form to *Stereogenys*. It can be thought of as derived from the pelomedusine pattern by general broadening of the shell, enlargement of the intergular and diminution of the gular shields. The humeral scales are separated by the intergular (fig. 15, F). The abdominal scute is narrow medially, but greatly expanded at the side, almost reaching from the axillary to the inguinal buttresses. In the carapace, the neural series is made up of seven plates, the first being suturally connected with the nuchal. The first vertebral

shield is broad, as in the pelomedusine type (fig. 14, C). Within the genus *Taphrosphys* there appears to be a line represented by *T. molops*, in which the gular shields are enlarged to meet at the midline in front of the intergular. The scale pattern of the carapace in *Amblypeza*, an extremely broad form, apparently close to *Taphrosphys*, curiously enough includes a nuchal shield, a character not observed in any other pelomedusid. Two lines within the genus *Podocnemis* can be derived from the pelomedusine pattern (fig. 15, G-K and L). In one the intergular and the gular scales are considerably smaller and the former particu-

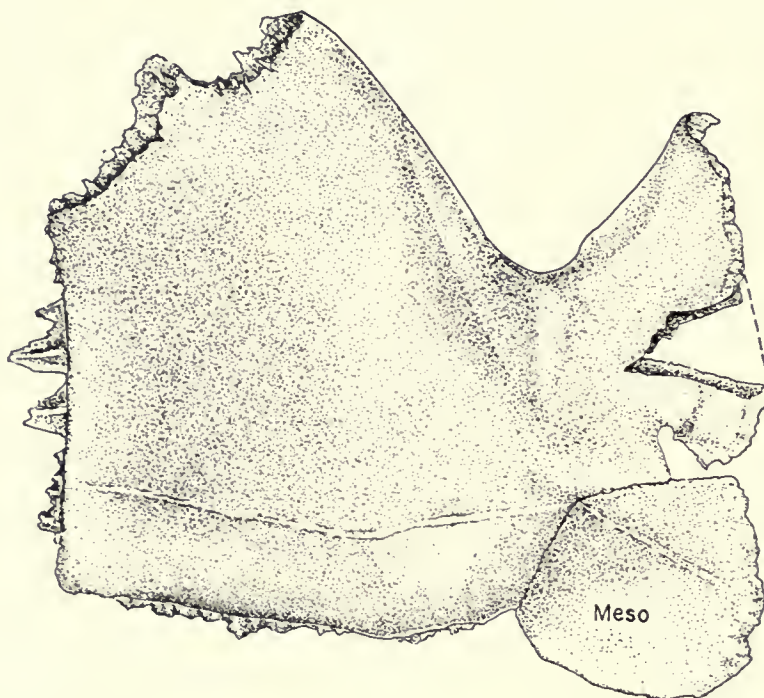


FIG. 10. Outer view of left hyo- and mesoplastron of *Podocnemis alabamae*, C.N.H.M. P27372. The pectoro-abdominal shield furrow is plainly visible.

larly narrow (*P. alabamae* and *P. brasiliensis*). The humero-pectoral sulci lie far forward about at mid-length of the entoplastron. The pectoro-abdominal furrows are either slightly advanced craniad and transgress onto the mesoplastra laterally (*P. alabamae*) or are considerably farther craniad on the hyoplastral plates (*P. brasiliensis*). The carapace includes seven neural plates in *P. brasiliensis*, six in *P. barberi*, and six or seven in *P. alabamae*. In all three of these species the lateral furrows of the first vertebral scute extend to the second marginal scales. This line, in which Tertiary intermediates are unknown, seems to lead to the living South American species. In these forms the normal number of neural plates is seven (rarely six), and the first vertebral shield is relatively narrow, extending laterally only to the first marginal scutes. If belief in a progressive reduction of the neurals in Pleurodira is correct, it appears that the Cretaceous North American forms are early side branches of the main line that have undergone reduction of the seventh neural plate.

In the second group comprising the Old World forms, the intergular becomes shorter, no longer than the gular shields, the humeral scales make no contact with the intergular, and the pectoro-abdominal furrows lie anterior to the mesoplastral plates. The neural series is reduced to six (*P. stromeri*). The conditions observed in *P. fajumensis*, *P. aegyptiaca*, and *P. madagascariensis* result from further diminution of the intergular so that the gular shields meet in the midline. *P. bramlyi* Fourtau from the Miocene of Egypt is peculiar in that the scale

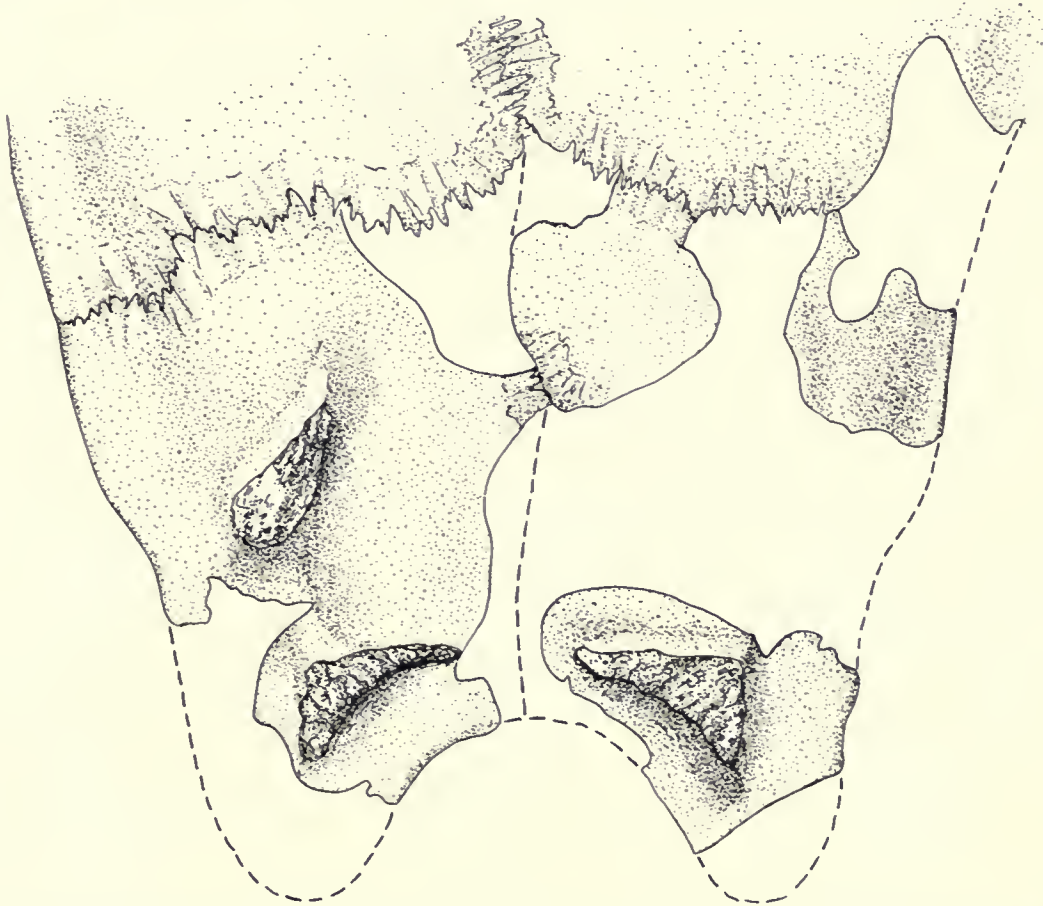


FIG. 11. Visceral view of xiphiplastral end of plastron of *Podocnemis alabamae*, C.N.H.M. P27370, showing shape and placement of ischial and pubic scars.

pattern on the anterior lobe of the plastron is essentially that of the New World representatives of the genus. Its geographic position and age, however, suggest (more complete knowledge of its organization is wanting) that it is derived from the *P. stromeri* pattern that paralleled the New World forms.

It seems clear that the Old and New World lines of *Podocnemis* have been separate at least as far back as the late Cretaceous.

The living genus *Pelomedusa*, represented in the Oligocene of Egypt by *P. progaleata* von Reinach, exhibits only slight modifications of the pelomedusine type. One of the outstanding features of this form is the thinness of the plastron,

which led, as far back as the Oligocene, to the formation of a central fontanelle between hyo- and hypoplastra. The shield pattern of the plastron is essentially that of *Podocnemis stromeri*, except that the humero-pectoral furrows lie, towards their medial ends, far behind the entoplastral bone. The pectoro-abdominal sulci are exactly as in the pelomedusine pattern. Save for proportional differences, the carapace compares very well with that of *Podocnemis stromeri*. In the Recent species *Pelomedusa galeata* a tendency toward reduction of the first neural plate is apparent. Thus, morphologically, *Pelomedusa* stands closer to the stem-line of *Podocnemis* than do *Stereogenys* and *Taphrosphys*. Haughton (1928) has described a turtle of uncertain age from Nyasaland (see also Stromer, 1934) as *Platycheloides nyasae* (fig. 15, D). This form shows a great deal of similarity to *Pelomedusa*, and would undoubtedly have been referred to this genus were it not for the lack of a central fontanelle in the plastron. Such a vacuity, however, must be regarded as a secondary development; apparently this form represents the most primitive member of the *Pelomedusa* line known to date.¹

In conclusion, it may be stated that, on the basis of evidence now at hand, the members of the family Pelomedusidae can be divided into two groups represented by the Pelusiinae and the Pelomedusinae. The latter can be subdivided into four major branches: *Stereogenys*, *Taphrosphys*, *Podocnemis*, and *Pelomedusa*.

Family PELOMEDUSIDAE

Pleurodiran turtles with eleven plastral bones, mesoplastra being present. Neural plates always present, varying from six to eight. Ilium in intimate contact with carapace; ischia and pubes firmly attached to plastron. A bony temporal arch; no parieto-squamosal arch; palatine bones in contact; no nasals; prefrontals in contact.

Subfamily PELUSIINAE

Mesoplastra large, in contact at midline; anterior lobe of plastron movable, a hinge being present between hyo- and mesoplastra.

Africa; Miocene to Recent.

Genus *Pelusios*.

Subfamily PELOMEDUSINAE

Mesoplastra small, laterally located; anterior lobe of plastron not movable.

Africa; Cretaceous(?)

North and South America; Late Cretaceous.

Congo; Paleocene.

Egypt, England, India, New Jersey, Peru; Eocene.

Egypt and Germany; Oligocene.

Egypt, Malta; Miocene.

Burma; Pliocene.

Africa, Madagascar, South America; Recent.

Genera: *Podocnemis*, *Pelomedusa*, *Platycheloides*, *Stereogenys*, *Taphrosphys*.

Tentatively referred genera: *Amblypeza*, *Dacochelys*, *Naiadochelys*, *Shweboemys*.

¹ The time of the segregation of the genera *Pelomedusa* and *Podocnemis* is not known but *Podocnemis* s.s. was already quite widely distributed in the late Cretaceous. The considerable degree of specialization of the genera *Stereogenys* and *Taphrosphys* in the Eocene suggests that the separation of all of these forms from the pelomedusine stem-line appears to have taken place before the end of the Cretaceous.

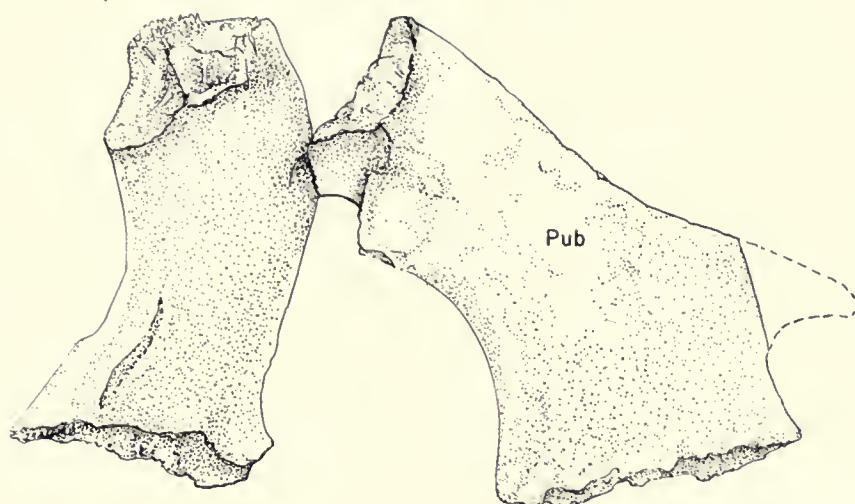


FIG. 12. Lateral view of right ischium and pubis of *Podocnemis alabamae*, C.N.H.M. P27370. The acetabular cavity is badly crushed.

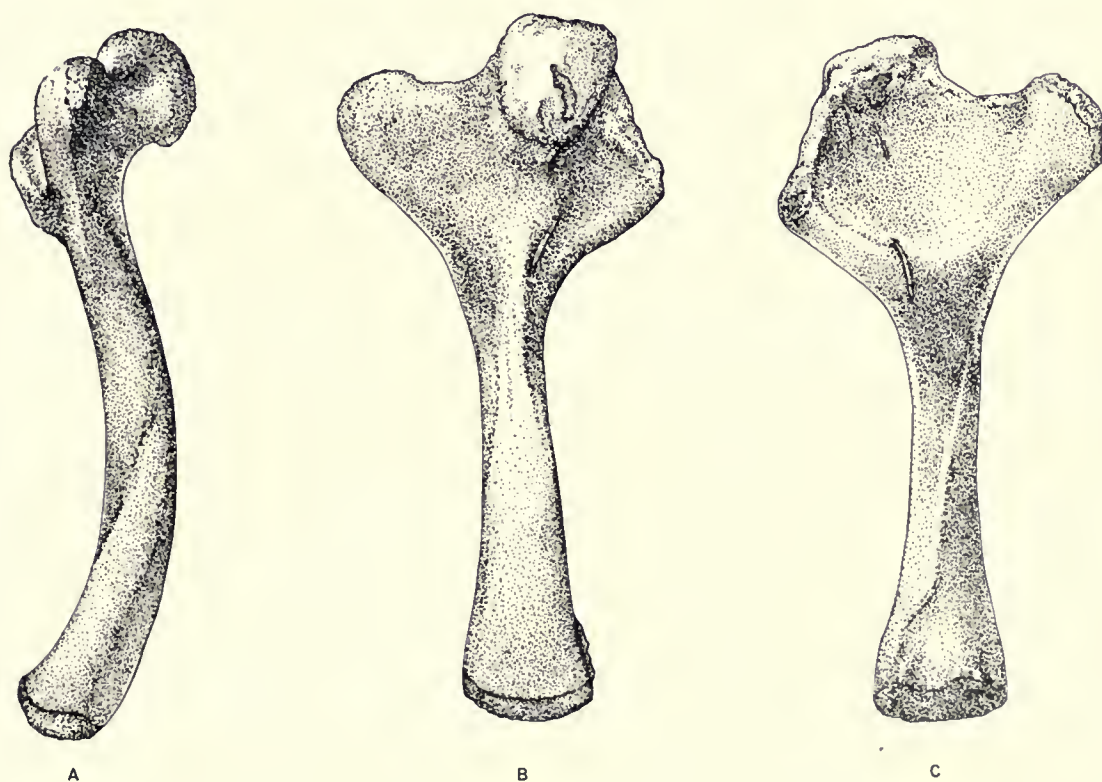


FIG. 13. Right humerus of *Podocnemis alabamae*, C.N.H.M. P27405. A, posterior view; B, dorsal view; C, ventral view.

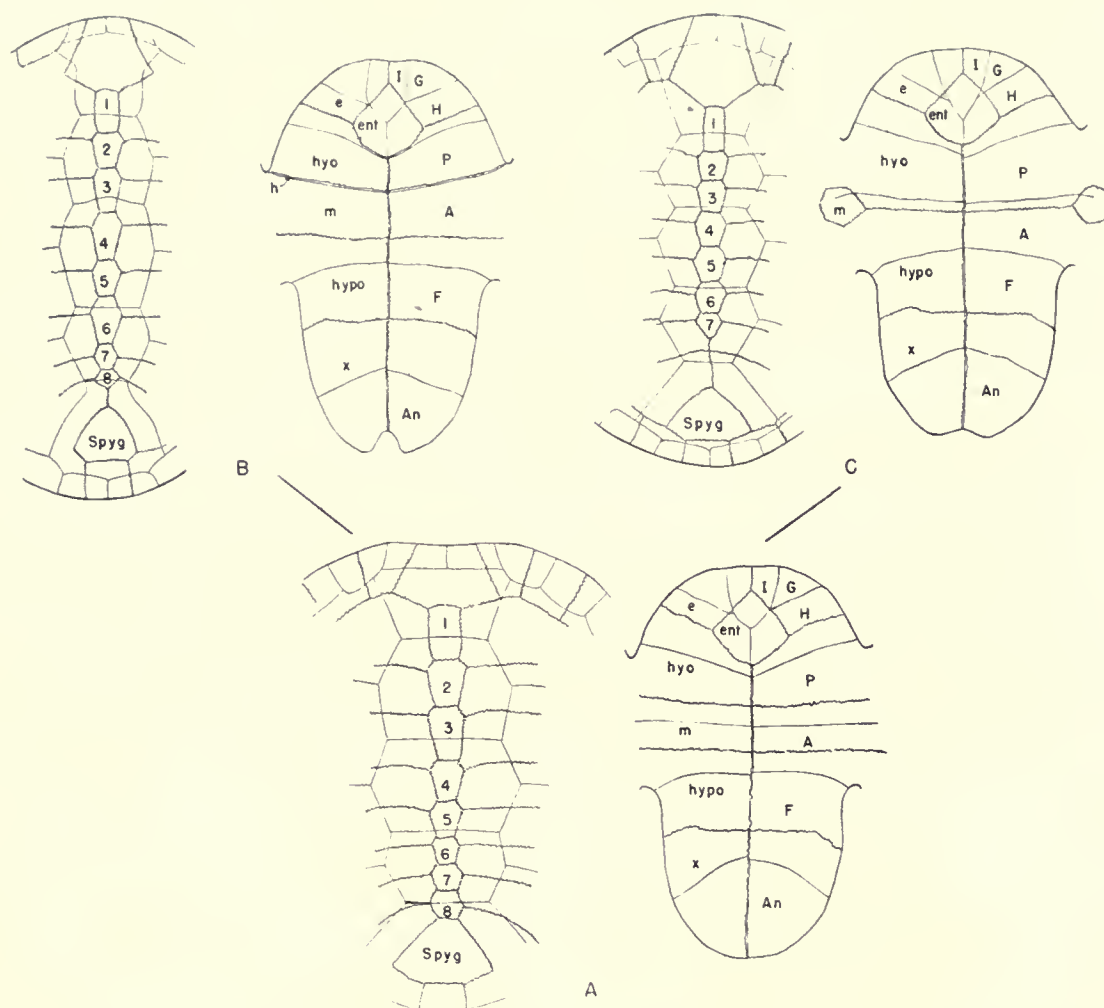


FIG. 14. A, morphological type pattern of pelomedusid shell; B, pelusiine type pattern; C, pelomedusine type pattern. The conditions illustrated in B and C can be morphologically derived from A.

e=epiplastron
ent=entoplastron
hyo=hyoplastron
m=mesoplastron
hypo=hypoplastron
x=xiphiplastron
Spyg=suprapygal
1, 2, etc.=neurals
I=intergular shield

G=gular shield
H=humeral shield
P=pectoral shield
A=abdominal shield
F=femoral shield
An=anal shield
h=hinge between mesoplastron and hyo-
 plastron

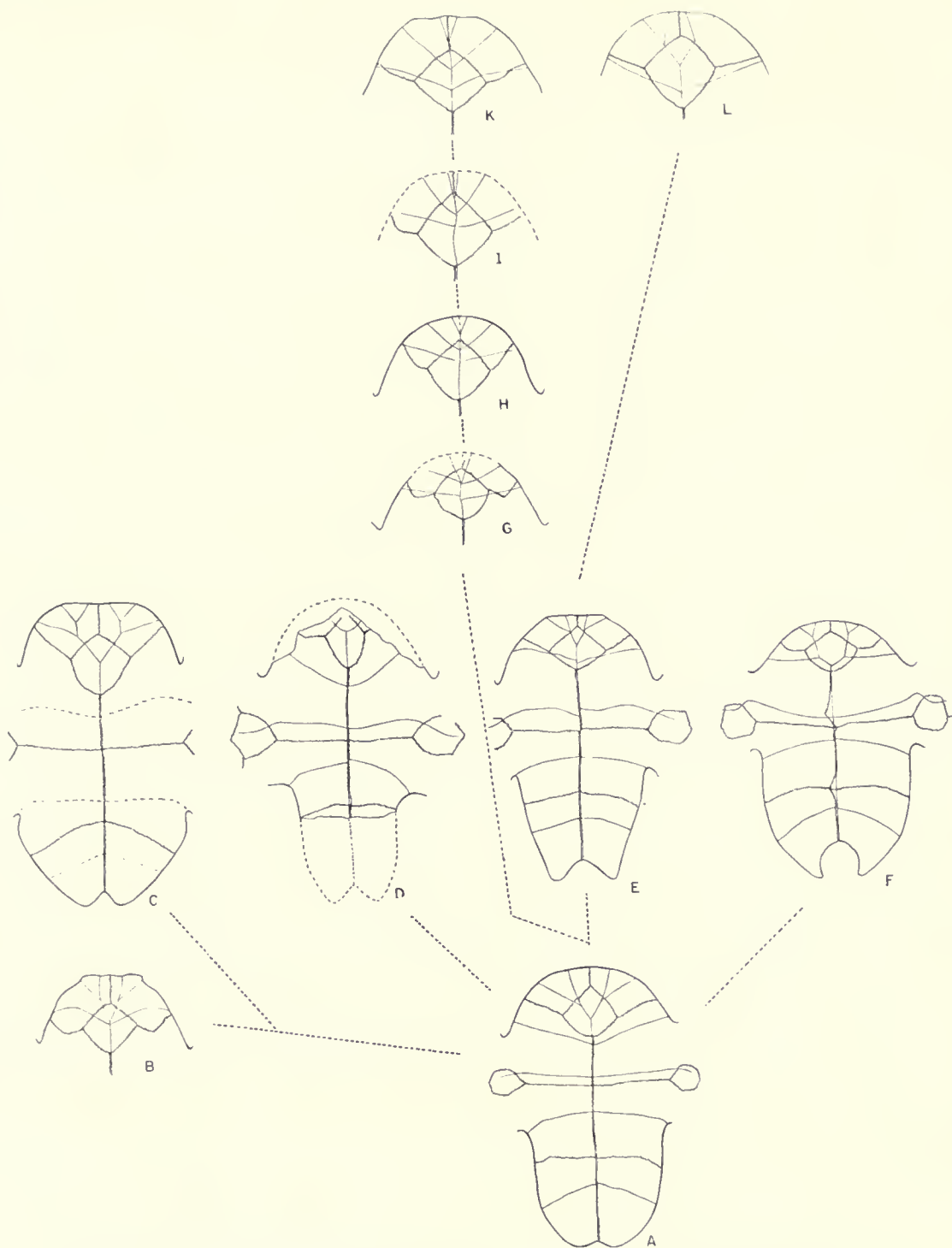


FIG. 15. Illustration of morphological affinities among pelomedusine turtles.

- | | |
|--|---|
| A. Pelomedusine type pattern. | F. <i>Taphrosphys olssoni</i> , representing the <i>Taphrosphys</i> branch. |
| B. <i>Stereogenys podocnemoides</i> , and | G. <i>Podocnemis stromeri</i> . |
| C. <i>Stereogenys cromeri</i> , representing the <i>Stereogenys</i> branch. | H. <i>Podocnemis fajumensis</i> . |
| D. <i>Platycheloides nyasae</i> , interpreted as a primitive member of the <i>Pelomedusa</i> branch. | I. <i>Podocnemis aegyptiaca</i> . |
| E. <i>Podocnemis alabamiae</i> , illustrating the <i>Podocnemis</i> branch. | K. <i>Podocnemis madagascariensis</i> . |
| | L. Pattern of living South American species of <i>Podocnemis</i> . |

The morphological affinities (fig. 16) among the pelomedusid turtles, as outlined above, are worked out on a sufficiently general basis so that major changes are not likely to be necessary in the future. More detailed relationships within the *Podocnemis* line cannot yet be accurately analyzed, because many forms are insufficiently known. This is true of the osteology of almost all Recent species, of *Podocnemis lata*, of *P. dehmi*, of *P. indica*, of *Bantuchelys congolensis* (= *Podocnemis? congolensis* Dollo), and of *Podocnemis harrisi*. *Podocnemis bowerbanki* and *Dacochelys delabechei* are relatively well-preserved specimens, but some of the features considered in the discussion above are unknown in both forms.

It may be pointed out that the interpretation of the mesoplastra as primitive elements of the turtle shell is at variance with Hay's (1908) idea that they, together with the peripheral plates, had been secondarily acquired by the Amphichelydia, Cryptodira, and Pleurodira. The early Mesozoic turtles have two pairs of mesoplastra, one of which disappears in the later Mesozoic forms. Among the latter, the mesoplastral elements may be retained or they may become partially or completely reduced, and without a doubt this process took place in different groups independently, for example, in the Cryptodira, in the Chelyidae, and in the Baenidae. Other cases of parallel modifications in the structural organization of the pelomedusids can readily be observed. *Taphrosphys* and *Stereogenys* resemble each other in the scale arrangement on the anterior plastral lobe. In an occasional specimen of the South American *Podocnemis dumeriliana* Schweigger the shield arrangement on the anterior lobe of the plastron duplicates that of *P. madagascariensis* (Siebenrock, 1902 and 1903), indicating a trend in the former species that, if permanently established, would constitute a parallel to the Old World line. The implied assumption of a closer genetic relationship of *P. dumeriliana* and the Madagascan species (Siebenrock, 1902; Müller, 1935) on the basis of this character and of some minor (and variable) features of the head, can, in view of the fossil record, scarcely be upheld. Yet another case of obvious parallelism can be observed in the numerical reduction of the neural series (see discussion above).

In the light of these observations it becomes increasingly necessary, particularly for the student of turtle morphology, to base his conclusions concerning structural affinities on as many anatomical features as are available for comparison, a challenge in line with a demand recently made by several morphologists who see the organism in its entirety—i.e. structure, physiology and behavior—instead of regarding it as a mosaic of more or less independent "characters."

SUMMARY

1. A new species of *Podocnemis* (*P. alabamæ*) from the late Cretaceous of Alabama is described. It is closely related to *Podocnemis barberi* from deposits of approximately the same age in Arkansas.

2. The basic pattern of the pelomedusid shell can be derived from the morphological type of the Pleurosternidae. Mesoplastra are regarded as primitive elements of the turtle shell.

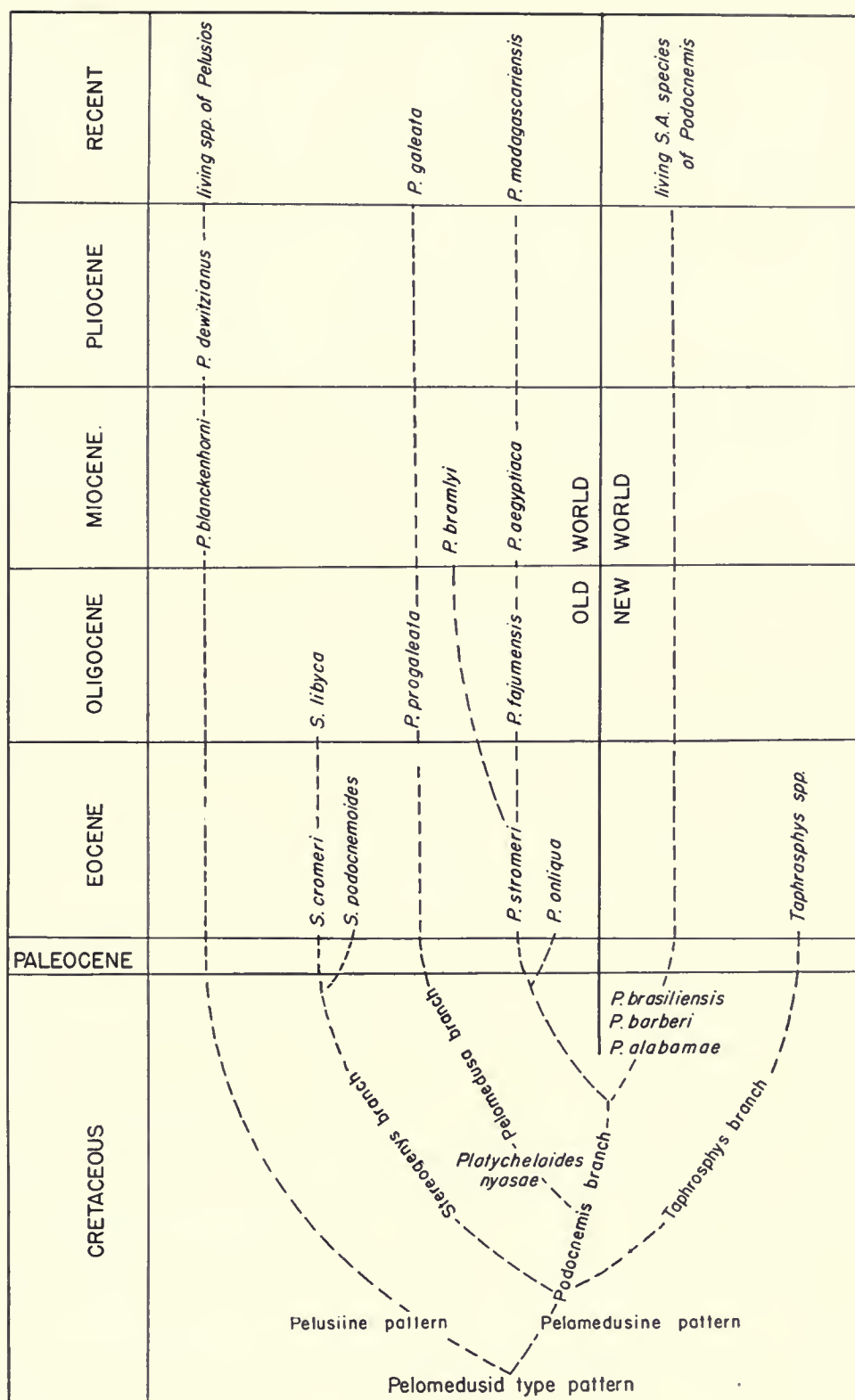


FIG. 16. Diagram showing morphological affinities among better-known pelomedusid turtles.

3. An analysis of the morphology of the shell in the pelomedusid turtles results in the recognition of two principal groups within the family Pelomedusidae: the Pelusiinae and the Pelomedusinae. *Stereogenys*, *Pelomedusa*, *Podocnemis*, and *Taphrosphys* are included in the pelomedusine group. There is a closer morphological affinity between *Pelomedusa* and *Podocnemis* than between either of these forms and *Stereogenys* or *Taphrosphys*.

4. Two lines can be recognized within the genus *Podocnemis*. One, well documented in the Tertiary of Egypt, leads to the living Madagascan species; the other, known from the American Cretaceous but lacking Tertiary intermediates to date, leads to the Recent South American species.

5. *Platycheloides nyasae* Haughton of uncertain age, from Nyasaland, is interpreted as a primitive relative of *Pelomedusa*.

6. *Podocnemis olssoni* from Peru belongs to the genus *Taphrosphys*, hitherto known only from the Green Sand beds of New Jersey.

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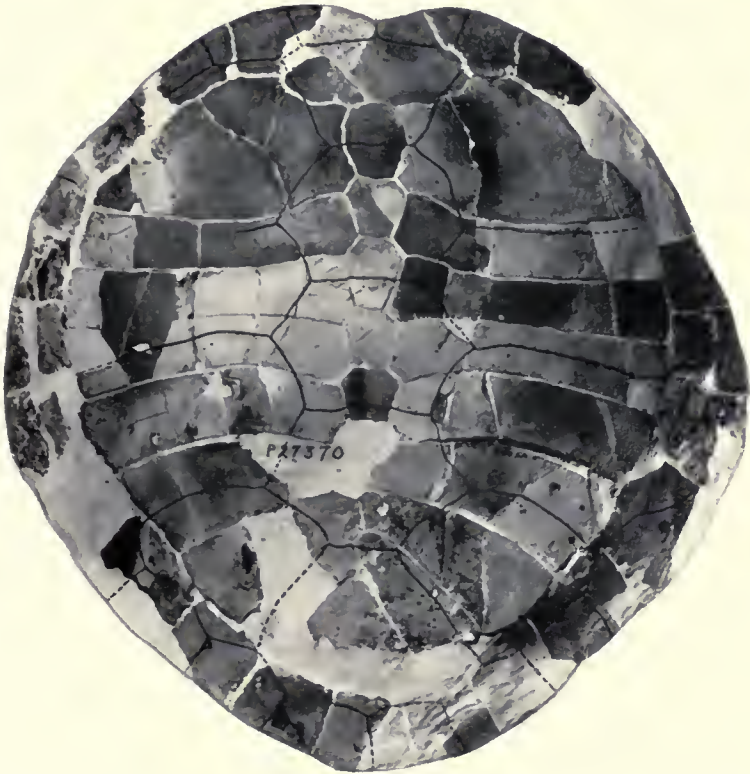
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EXPLANATION OF PLATE 4

FIG. 1.—Carapace of *Podocnemis alabamae*, C.N.H.M. P27370 (holotype).

FIG. 2.—Visceral view of plastron of *Podocnemis alabamae*, C.N.H.M. P27369; *m*=mesoplastron.

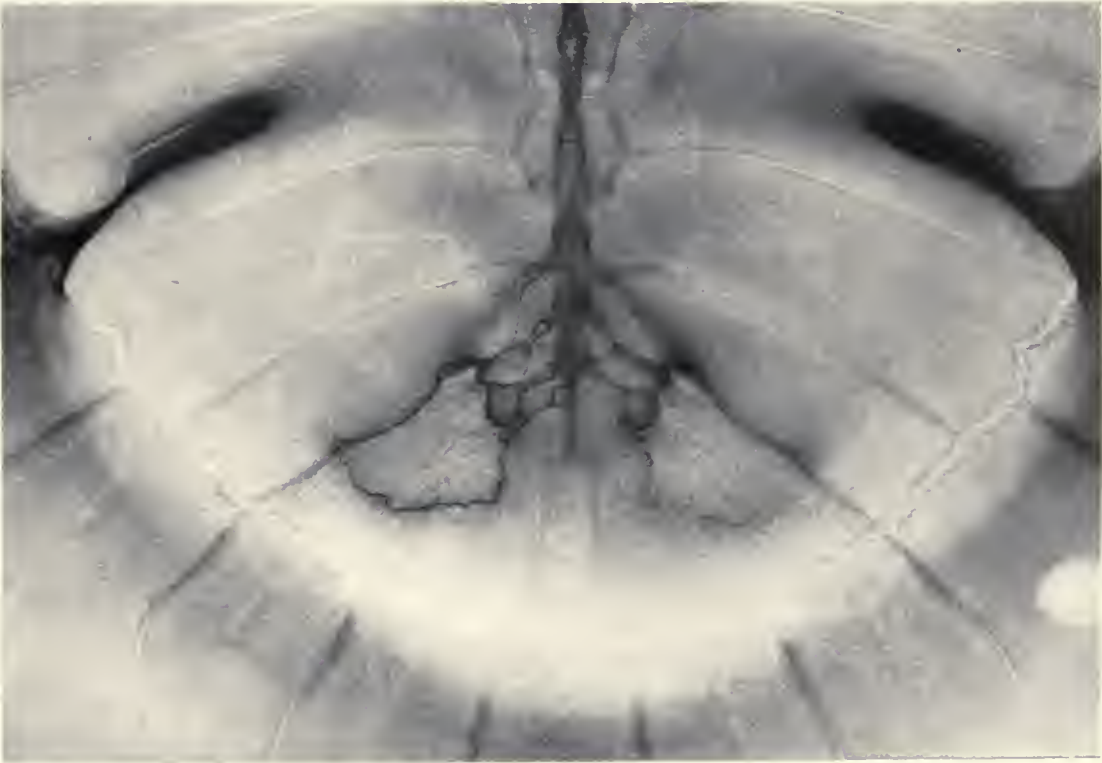
FIG. 3.—X-ray photograph of posterior (sacral) part of shell of *Podocnemis expansa*, C.N.H.M. 16075, for comparison with text figures 6 and 9. The similarity in the arrangement of the sacral ribs between this species and *P. alabamae* is evident. The last sacral vertebra and its ribs are broken off. On the left side of the plate the sacral ribs are outlined in ink, the last one reconstructed. The distal end of the fourth sacral rib is visible on the right side of the plate.



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